UNIVERSITÉ DU QUÉBEC À MONTRÉAL

CARBON DYNAMICS AND MANAGEMENT IN CANADIAN BOREAL FORESTS: TRIPLEX-FLUX MODEL DEVELOPMENT, VALIDATION, AND APPLICATIONS

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DYNAMIQUE DU CARBONE ET GESTION DE LA FORET BOREALE DU CANADA: DEVELOPPEMENT, VALIDATION ET APPLICATION POUR LE MODELE TRIPLEX-FLUX

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PREFACE

The following seven manuscripts are synthesized to present my research in this dissertation:

Chapter II Zhou, X., Peng, C., Dang, Q.-L., Sun, J.F., Wu, H. and Hua, D. 2008 Simulating carbon exchange of Canadian boreal forests I: Model structure, validation, and sensitivity analysis. *Ecological Modelling*, 219 (3-4): 276-286.

Chapter III Sun, J.F, Peng, C., McCaughey, H., Zhou, X., Thomas, V., Berninger, F., St-Onge, B. and Hua, D. 2008. Simulating Carbon Exchange of Canadian Boreal Forests II: Comparing the carbon budgets of a boreal mixedwood stand to a black spruce forest stand. *Ecological Modelling*, 219 (3-4): 287-299.

Chapter IV Sun, J.F., Peng, C.H., Zhou, X.L., Wu, H.B., St-Onge, B. Parameter estimation and net ecosystem productivity prediction applying the model-data fusion approach at seven forest flux sites across North America. To be submitted to *Environment Modelling & Software.*

Chapter V Sun, J.F., Peng, C.H., St-Onge, B. Carbon dynamics, maturity age, and stand density management diagram of black spruce forests stands located in eastern Canada: a case study using the TRIPLEX model. To be submitted to *Canadian Journal of Forest Research.*

APPENDIX 1 G.R. Larocque, J.S. Bhatti, A.M. Gordon, N. Luckai, M. Wattenbach, J. Liu, C. Peng, P.A. Arp, S. Liu, C.-F. Zhang, A. Komarov, P. Grabarnik, J.F. Sun and T. White. 2008. Uncertainty and Sensitivity Issues in Process-based Models of Carbon and Nitrogen Cycles in Terrestrial Ecosystems In: A.J. Jakeman et al., editors, Developments in Integrated Environmental Assessment vol. 3. Environmental Modelling, Software and Decision Support. p.307-327, Elsevier Science.

APPENDIX 2 Lei, X., Peng, C.H., Tian, D., and Sun, J.F. 2007. Meta-analysis and its application in global change research. *Chinese Science Bulletin,* 52: 289-302.

APPENDIX 3 Sun, J.F., Peng, C.H., St-Onge, B, Lei, X. Application of meta-analysis in quantifying the effects of soil warming on soil respiration in forest ecosystems. To be submitted to *Journal of Plant Ecology*.

CO-AUTHORSHIP

For the papers in which I am the first author, I was responsible for setting up the hypothesis, the research methods and ideas, study area selection, model development and validation, data analysis and manuscript writing.

For the others, I was active in programming to develop the model using C++, model simulation, data analysis and manuscript preparation.

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RÉSUMÉ

La forêt boréale, seconde aire biotique terrestre sur Terre, est actuellement considerée comme un réservoir important de carbone pour l'atmosphère. Les modèles basés sur le processus des écosytèmes terrestres jouent un rôle important dans l'écologie terrestre et dans la gestion des ressources naturelles. Cette thèse examine le développement, la validation et l'application aux pratiques de gestion des forêts d'un tel modèle.

Tout d'abord, le module récement développé d'échange du carbone TRIPLEX-Flux (avec des intervalles de temps d'une demi heure) est utilisé pour simuler les échanges de carbone des écosystèmes d'une forêt au peuplement boréal et mixte de 75 ans dans le nord est de l'Ontario, d'une forêt avec un peuplement d'épinette noire de 110 ans localisée dans le sud de Saskatchewan, et d'une forêt avec un peuplement d'épinette noire de 160 ans située au nord du Manibota au Canada. Les résultats des échanges nets de l'écosystème (ENE) simulés par TRIPLEX-Flux sur l'année 2004 sont comparés à ceux mesurés par les "tours de mesures de covariance des turbulences" et montrent une bonne correspondance générale entre les simulations du modèle et les observations de terrain. Le coefficient de détermination moyen (R^2) est approximativement de 0.77 pour le peuplement mixte boréal, et de 0.62 et 0.65 pour les deux forêts d'épinette noire situées au centre du Canada. Le modèle est capable d'intégrer les variations diurnes de l'échange net de l'écosystème (ENE) de la période de pousse (de mai à août) de 2004 sur les trois sites. Le peuplement boréal mixte ainsi que les peuplements d'épinette noire agissaient tous deux comme des réservoirs de carbone pour l'atmosphère durant la période de pousse de 2004. Cependant le peuplement boréal mixte montre une plus grande productivité de l'écosystème, un plus grand piégeage du carbone ainsi qu'un meilleur taux de carbone utilisé comparé aux peuplements d'épinette noire.

L'analyse de la sensibilité a mis en évidence une différence de sensibilité entre le matin et le milieu de journée, ainsi qu'entre une concentration habituelle et une concentration doublée de CO_2. De plus, la comparaison de différents algorithmes pour calculer la conductance stomatale a montré que la production nette de l'écosystème (PNE) modelisée, utilisant une itération d'algorithme est conforme avec les résultats utilisant des rapports Ci/Ca constants de 0.74 et de 0.81 respectivement pour les concentrations courantes et doublées de CO_2. Une variation des paramètres et des données variables de plus ou moins 10% a entrainé, respectivement pour les concentrations courantes et doublées de CO_2, une réponse du modèle inférieure ou égale à 27.6% et à 27.4%. La plupart des paramètres sont plus sensibles en milieu de journée que le matin excepté pour ceux en lien avec la température de l'air, ce qui suggère que la température a des effets considérables sur la sensibilité du modèle pour ces paramètres/variables. L'effet de la température de l'air était plus important dans une atmosphère dont la concentration de CO_2 était doublée. En revanche, la sensibilité du modèle au CO_2 qui diminuait lorsque la concentration de CO_2 était doublée.

Sachant que, les incertitudes de prédiction des modèles proviennent majoritairement

des hétérogeneities spacio-temporelles au coeur des écosystèmes terrestres, à la suite du développement du modèle et de l'analyse de sa sensibilité, sept sites forestiers à tour de mesures de flux (comportant trois forêts à feuilles caduques, trois forêts tempérées à feuillage persistant et une forêt boréale à feuillage persistant) ont été selectionnés pour faciliter la compréhension des variations mensuelles des paramètres du modèle. La méthode de Monte Carlo par Markov Chain (MCMC) à été appliquée pour estimer les paramètres clefs de la sensibilité dans le modèle basé sur le processus de l'écosystème, TRIPLEX-Flux. Les quatre paramètres clefs sélectionnés comportent: un taux maximum de carboxylation photosynthétique à 25°C (Vmax), un taux du transport d' un électron (Jmax) saturé en lumière lors du cycle photosynthétique de réduction du carbone , un coefficient de conductance stomatale (m), et un taux de référence de respiration à 10°C (R_{10}). Les mesures de covariance des flux turbulents du CO_2 échangé ont été assimilées afin d'optimiser les paramètres pour tous les mois de l'année 2006. Après que l'optimisation et l'ajustement des paramètres ait été réalisée, la prédiction de la production nette de l'écosystème s'est ameliorée significativement (d'environ 25%) en comparaison avec les mesures de flux de CO_2 réalisés sur les sept sites d'écosystèmes forestiers. Les résultats suggèrent, dans le respect des paramètres sélectionnés, qu'une variabilité plus importante se produit dans les forêts à feuilles larges que dans les forêts d'arbres à aiguilles. De plus, les résultats montrent que l'approche par la fusion des données du modèle incorporant la méthode MCMC peut être utilisée pour estimer les paramètres basés sur les mesures de flux, et que des paramètres saisonniers optimisés peuvent considérablement améliorer la précision d'un modèle d'écosystème lors de la simulation de sa productivité nette et cela pour différents écosystèmes forestiers situés à travers l'Amerique du Nord.

Finalement, quelques uns de ces paramètres et algorithmes testés ont été utilisés pour mettre à jour l'ancienne version de TRIPLEX comportant des intervalles de temps mensuels. En outre, le volume d'un peuplement et la quantité de carbone de la biomasse au dessus du sol des forêts d'épinette noire au Québec sont simulés en relation avec un peuplement des âges, cela à des fins de gestion forestière. Ce modèle a été validé en utilisant à la fois une tour de mesure de flux et des données d'un inventaire forestier. Les simulations se sont averrées réussies. Les corrélations entre les données observées et les données simulées (R^2) étaient de 0.94 0.93 et 0.71 respectivement pour le diamètre à 1.3m, la moyenne de la hauteur du peuplement et la productivité nette de l'écosystème. En se basant sur les résultats à long terme de la simulation, il est possible de déterminer l'âge de maturité du carbone du peuplement consideré comme prenant place à l'époque où le peulement de la forêt prélève le maximum de carbone, avant que la récolte finale ne soit realisée. Après avoir comparé l'âge de maturité du volume des peuplements considérés (d'environ 65 ans) et l'âge de maturité du carbone des peulpements considérés (d'environ 85ans), les résultats suggèrent que la récolte d'un même peuplement à son âge de maturité de volume est prématuré. Décaler la récolte d'environ vingt ans et permettre au peuplement considéré d'atteindre l'âge auquel sa maturité du carbone prend place, ménera à la formation d'un réservoir potentiellement important de carbone. Aussi, un nouveau diagramme de la gestion de la densité du carbone du peuplement considéré, basé sur les résultats de la simulation, a été développé pour démontrer quantitativement les relations entre les

densités de peuplement, le volume de peuplement et la quantité de carbone de la biomasse au dessus du sol à des stades de développement variés, dans le but d'établir des régimes de gestion de la densité optimaux pour le rendement de volume et le stockage du carbone.

Mots-Clefs: écosystème forestier, flux de CO_2, production nette de l'écosystème, eddy covariance, TRIPLEX-Flux module, validation d'un modèle, Markov Chain Monte Carlo, estimation des paramètres, assimilation des données, maturité du carbone, diagramme de gestion de la densité de peuplement

ABSTRACT

The boreal forest, Earth's second largest terrestrial biome, is currently thought to be an important net carbon sink for the atmosphere. Process-based terrestrial ecosystem models play an important role in terrestrial ecology and natural resource management. This thesis focuses on TRIPLEX model development, validation and application of the model to carbon sequestration and budget as well as on forest management practices impacts in Canadian boreal forest ecosystems.

Firstly, this newly developed carbon exchange module of TRIPLEX-Flux (with half-hourly time step) is used to simulate the ecosystem carbon exchange of a 75-year-old boreal mixedwood forest stand in northeast Ontario, a 110-year-old pure black spruce stand in southern Saskatchewan, and a 160-year-old pure black spruce stand in northern Manitoba, Canada. Results of net ecosystem exchange (NEE) simulated by this model for 2004 are compared with those measured by eddy flux towers and suggest good overall agreement between model simulation and observations. The mean coefficient of determination (R^2) is approximately 0.77 for the boreal mixedwood, 0.62 and 0.65 for the two old black spruce forests in central Canada. The model is able to capture the diurnal variations of NEE for the 2004 growing season in these three sites. Both the boreal mixedwood and old black spruce forests were acting as carbon sinks for the atmosphere during the 2004 growing season. However, the boreal mixedwood stand shows higher ecosystem productivity, carbon sequestration, and carbon use efficiency than the old black spruce stands.

The sensitivity analysis of TRIPLEX-flux module demonstrated different sensitivities between morning and noon, and from current to doubled atmospheric CO_2 concentrations. Additionally, the comparison of different algorithms for calculating stomatal conductance shows that the modeled NEP using the iteration algorithm is consistent with the results using a constant C_i/C_a of 0.74 and 0.81, respectively for the current and doubled CO_2 concentration. Varying parameter and input variable values by ±10% resulted in the model response to less than and equal to 27.6% and 27.4% for morning and noon, respectively. Most parameters are more sensitive at noon than in the morning except those that are correlated with air temperature suggesting that air temperature has considerable effects on the model sensitivity to these parameters/variables. The air temperature effect was greater under doubled than current atmospheric CO_2 concentration. In contrast, the model sensitivity to CO_2 decreased under doubled CO_2 concentration.

Since prediction uncertainties of models stems mainly from spatial and temporal heterogeneities within terrestrial ecosystems, after the module development and sensitivity analysis, seven forest flux tower sites (including three deciduous forests, three evergreen temperate forests, and one evergreen boreal forest) were selected to facilitate understanding of the monthly variation in model parameters. The Markov Chain Monte Carlo (MCMC) method was applied to estimate sensitive key parameters in this TRIPLEX-Flux process-based ecosystem module. The four key parameters

selected include a maximum photosynthetic carboxylation rate of 25°C (V_{max}), an electron transport (J_{max}) light-saturated rate within the photosynthetic carbon reduction cycle of leaves, a coefficient of stomatal conductance (m), and a reference respiration rate of 10°C (R_{10}). Eddy covariance CO_2 exchange measurements were assimilated to optimize the parameters for each month in 2006. After parameter optimization and adjustment took place, the prediction of net ecosystem production significantly improved (by approximately 25%) compared to the CO_2 flux measurements taken at these seven forest ecosystem sites. Results suggest that greater seasonal variability occurs in broadleaf forests in respect to the selected parameters than in needleleaf forests. Moreover, results show that the model-data fusion approach incorporating the MCMC method can be used to estimate parameters based upon flux measurements, and that optimized seasonal parameters can greatly improve ecosystem model accuracy when simulating net ecosystem productivity for different forest ecosystems located across North America.

Finally, some of these well-tested parameters and algorithms were used to update and improve the old version of TRIPLEX1.0 that used monthly time steps. Furthermore, stand volume and the aboveground biomass carbon quantity of black spruce (*Picea mariana*) forests in Québec are simulated in relation to stand age for forest management purpose. The model was validated using both a flux tower and forest inventory data. Simulations proved successful. The correlations between observational data and simulated data (R^2) are 0.94, 0.93, and 0.71 for diameter at breast height (DBH), mean stand height, and net ecosystem productivity (NEP), respectively. Based on these long-term simulation results, it is possible to determine the age of forest stand carbon maturity that is believed to take place at the time when a stand uptakes the maximum amount of carbon before final harvesting occurs. After comparing the stand volume maturity age (approximately 65 years old) with the stand carbon maturity age (approximately 85 years old), results suggest that harvesting a stand at its volume maturity age is premature for carbon. Postponing harvesting by approximately 20 years and allowing the stand to reach the age at which carbon maturity takes place may lead to the formation of a potentially large carbon sink. Also, based on the simulation results, a novel carbon stand density management diagram (CSDMD) has been developed to quantitatively demonstrate relationships between stand densities and stand volume and aboveground biomass carbon quantity at various stand developmental stages in order to determine optimal density management regimes for volume yield and carbon storage.

Keywords: forest ecosystem, CO_2 flux, net ecosystem production, eddy covariance, TRIPLEX-Flux, model validation, Markov Chain Monte Carlo, parameter estimation, data assimilation, carbon maturity, stand density management diagram

摘　　要

北方针叶林作为第二大的陆地生态系统目前被认为一个是非常重要的大气净碳汇。过程模型在陆地生态学和自然资源管理方面发挥着非常重要的作用。这篇毕业论文将重点讨论TRIPLEX模型关于碳循环模拟的开发和验证，及其在加拿大北方针叶林生产管理过程中的应用。

这个新开发的TRIPLEX（半小时步长）碳通量模块被首先应用于安大略省东北部（一个75年林龄的混交林），萨斯喀彻温省南部（一个110年林龄的云杉纯林）以及马尼托巴省北部（一个160年林龄的云杉纯林）。通过与2004年的碳通量塔观测结果比较，R^2分别是0.77，0.62和0.65。模拟与观测结果总体上是一致的，该模型在加拿大北方针叶林能够捕捉到每天碳通量的变化动态。在2004年的生长季，混交林和云杉林都起到了大气的碳汇作用。但是，混交林具有更高的生态系统净生产力和固碳效率。

敏感性分析结果表明在早晨与中午、当前与倍增的大气二氧化碳浓度条件下，模型的敏感程度具有差异性。此外，在当前和大气二氧化碳浓度倍增情况下，气孔导度模型的迭代算法与Ci/Ca为常量（分别是0.74和0.81）的净生态系统生产力（NEP）结果基本上一致的。±10%的参数和变量变化导致模拟结果小于或等于27.6% （早晨）和27.4（中午）的变动。除了与气温密切相关的多数参数在中午更为敏感。与模型的敏感性相反，大气二氧化碳浓度倍增时，气温的敏感性更大。

模型的不确定性主要源于陆地生态系统的时空间差异性，在七个森林（三种林型）碳通量塔站，蒙特卡罗马尔可夫链 （MCMC）方法被用于四个主要敏感参数的月变化检验，包括Vmax、 Jmax、气孔导度参数和土壤呼吸参数。通过2006年的通量塔观测数据同化和参数估计，NEP模拟结果被提高了25%。从而，MCMC方法可以应用于北美不同的森林类型。阔叶林对这些参数更敏感。

最后，这些经过验证的算法和参数被用于改进TRIPLEX 1.0。该模型被碳通量塔和森林调查数据验证后，用于魁北克云杉林的长期动态模拟和森林管理。胸径，树高及NEP的R^2分别是0.94、0.93和0.71。因为碳成熟（85年）比数量成熟（65年）晚20年，从而森林主伐也应该相应地延长。基于模拟结果，新绘制的碳密度控制管理图可应用于各林龄阶段的森林密度管理。

关键词：森林生态系统，碳通量，净生态系统生产力，涡度相关，TRIPLEX-Flux，模型验证，蒙特卡罗马尔可夫链，参数估计，数据同化，碳成熟，密度控制管理图

CHAPTER I

GENERAL INTRODUCTION

1.1. BACKGROUND

Boreal forests form Earth's second largest terrestrial biome and play a significant role in the global carbon cycle, because boreal forests are currently thought to be important net carbon sinks for the atmosphere (Tans et al., 1990; Ciais et al., 1995; Sellers et al., 1997; Fan et al., 1998; Gower et al, 2001; Bond-Lamberty et al., 2004; Dunn et al., 2007). Canadian boreal forests account for about 25% of the global boreal forest and nearly 90% of the productive forest area in Canada.

Since the beginning of the Industrial Revolution, increasing human activities have increased CO_2 concentration in the atmosphere and the temperature to increase (IPCC, 2001, 2007). The boreal forest ecosystem has long been recognized as an important global carbon sink, however, the pattern and mechanism responsible for this carbon sink is uncertain. Although some study areas of forest productivity are still poorly represented, a review of the relevant literature (see Fig. 1.1) suggests that there is a reasonable carbon budget of the boreal forest ecosystem at the global scale here. Actually, because of the high degree of spatial heterogeneity in sinks and sources, as well as the anthropogenic influence on the landscape, it is particularly difficult to determine the role of the boreal forest in the global carbon cycle.

Temperature of the boreal forest varies from –45 °C to 35 °C (Bond-Lamberty et al, 2005), and annual mean precipitation is 900mm (Fisher and Bonkley, 2000). However, unlike temperate forest ecosystems, the boreal forest is more sensitive to spring warming and spring time freeze events (Hollinger et al, 1994; Goulden et al, 1996; Hogg et al, 2002; Griffis et al, 2003; Tanja et al, 2003; Barr et al, 2004). Actually, climate change could have a wider array of impacts on forests in North America,

including range shifts, soil properties, tree growth, disturbance regimes, and insect and disease dynamics (Evans and Perschel, 2009).

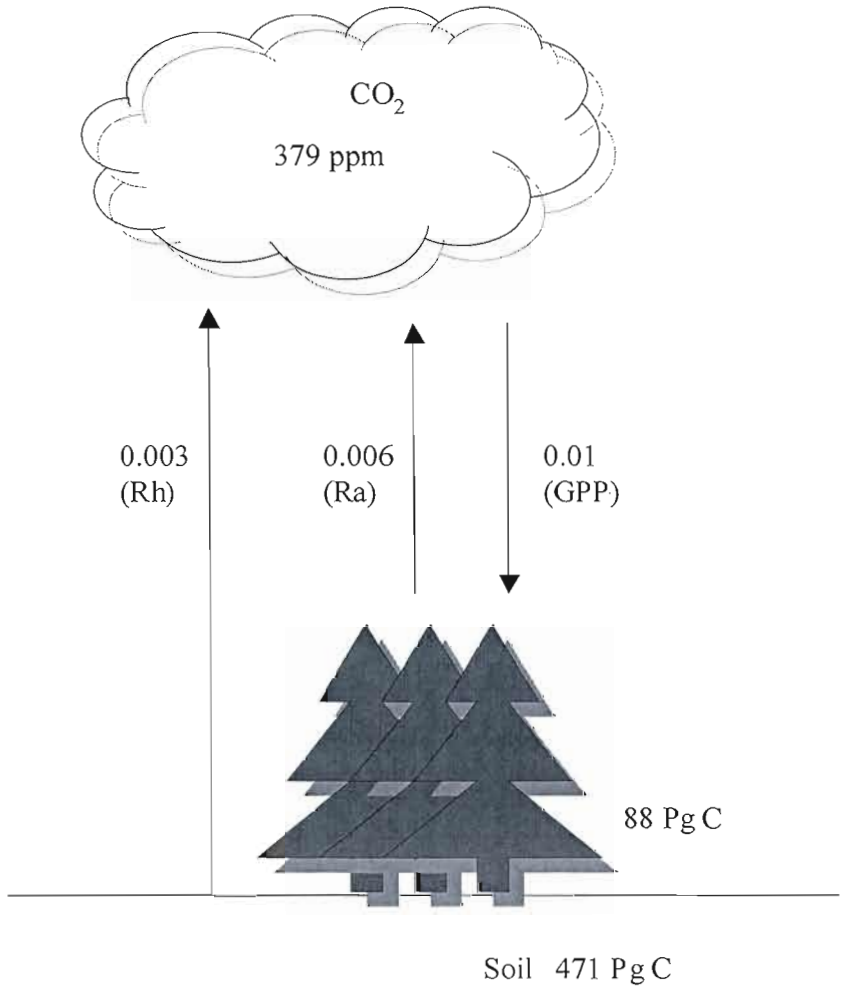

Fig. 1.1. Carbon exchange between the global boreal forest ecosystems and atmosphere, adapted from IPCC (2007), Prentice (2001) and Luyssaert et al. (2007). Rh: Heterotrophic respiration; Ra: Autotropic respiration; GPP: Gross primary production.

There is conflicting evidence as to whether Canadian boreal forest ecosystems are currently a sink or a source for CO_2. For example, the Carbon Budget Model of the Canadian Forest Sector estimated that Canadian forests might currently be a small source because of enhanced disturbances during the last three decades (Kurz and Apps 1999; Bond-Lamberty et al., 2007; Kurz et al., 2008). In contrast, BEPS-InTEC model estimated that Canadian forests are a small C sink (Chen et al. 2000). Myneni et al. (2001) combined remote sensing with provincial inventory data to demonstrate that Canadian forests have been an average carbon sink of ~0.07 Gt/yr for the last two decades. Unfortunately, previous attempts to quantitatively assess the effect of changing environmental conditions on the net boreal forest carbon balance have not taken into account competition between different vegetation types, forest management practices (harvesting and thinning), land use change, and human activities on a large scale.

1.2. MODEL OVERVIEW

There are three approaches used to assess the effects of changing environmental on forest dynamics and carbon cycles (Botkin, 1993; Landsberg and Gower 1997,): (1) our knowledge of the past, (2) present measurements, and (3) our ability to project into the future. Our knowledge of the past and present measurements are potentially important, but have been of limited use. Long-term monitoring of the forest has proven difficult due to costs and the need for long-term commitment of individuals and institutions. Because the response of temporal and spatial patterns of forest structure and function to changing environment involves complicated biological and ecological mechanisms, current experimental techniques are not directly applicable. In contrast, models provide a means of formalizing a set of hypotheses.

To improve our understanding of terrestrial ecosystem responses to climate change, models are applied widely to simulate the effects of climate change on production, decomposition and carbon balance in boreal forests in recent years.

1.2.1. Model types:

So far, three types of models, empirical, mechanistic, and hybrid models are popular for forest ecological and climate change studies (Peng et al, 2002; Kimmins, 2004). Using forest measurements and observations, site dependent empirical models (e.g., forest growth and yield models) are widely applied for forest management purposes because of their simplicity and feasibility. However, these models are only suitable for predicting in the short-term and at the local scale, and lack flexibility to account for forest damage evaluation of a sudden catastrophe (e.g., ice storm or fire) as well as long-term environment changes (e.g. increasing temperature and CO_2 concentration).

Unlike empirical models, process models are generally developed after a certain amount of knowledge has been accumulated using empirical models, and may describe a key ecosystem process or simulate the dependence of growth on a number of interacting processes, such as photosynthesis, respiration, decomposition, and nutrient cycling. These models offer a framework for testing and generating alternative hypotheses and have the potential to help us to accurately describe how these processes will interact under given environmental change (Landsberg and Gower, 1997). Consequently, their main contributions include the use of eco–physiological principles in deriving model development and specification, and long–term forecasting applicability within changing environments (Peng, 2000). Currently, the complex process-based models, although with long-term forecasting capacity in changing environment, are impossible to use to guide forest silviculture and management planning, and they still are only used in forest ecological research as a result of the need for lumped input parameters.

BEPS-InTEC (Liu et al, 1997; Chen et al. 1999, 2000), CLASS (Verseghy, 2000), ECOSYS (Grant, 2001) and IBIS (Foley, 1996) are the principal process-based models with hourly or daily time steps in use in the Fluxnet-Canada network. A critique of each model follows. (1) The Boreal Ecosystem Productivity Simulator (BEPS), derived from the FOREST-BGC model family, together with the Integrated Terrestrial Ecosystem Carbon Cycle Model (InTEC), is able to simulate net primary productivity (NPP), net ecosystem productivity (NEP) and evapotranspiration at the regional scale.

This model requires as input leaf area index (LAI) and land-cover type from remote sensing data plus some other environmental data (e.g., meteorological data and soil data). However, this kind of BGC model only considers the impacts of vegetation cover change on the climate, but ignores the impacts of climate change on vegetation cover change. (2) The Canadian Land Surface Scheme (CLASS) was developed by the Meteorological Service of Canada (MSC) to couple with the Canadian General Climate Model (CGCM). At the stand level, this biophysical land surface parameterization (LSP) scheme is designed to simulate the exchange of energy, water, and momentum between the surface and the atmosphere using prescribed vegetation and soil characteristics (Bartlett et al, 2003), but it neglects vegetation cover change (Foley, 1996; Wang et al, 2001; Arora 2003). Recently, like most similar models, new routines have been integrated into CLASS to simulate carbon and nitrogen dynamics in forest ecosystems (Wang et al, 2002). (3) ECOSYS is developed to simulate carbon, water, nutrient, and energy cycles in the multiple canopy layers divided into sunlit and shade leaf components and with a multilayered soil. Although prepared to elucidate the impacts of climate, land use practices and soil management (e.g., fertilization, tillage, irrigation, planting, harvesting, thinning) (Hanson 2004) and tested in U.S.A., Europe and Canada (Grant 2001), this model is too complicated to apply to forest management activities. (4) The Integrated BIosphere Simulator (IBIS) is an hourly Dynamic Global Vegetation Model (DGVM) developed at Wisconsin university (Kucharik et al, 2000) and has been adapted by CFS at regional and national scales. This model includes land surface processes (energy, water, carbon and momentum balance), soil biogeochemistry, vegetation dynamics (light, water and nutrients competition), and vegetation phenology modules. But this model neglects leaf nitrogen content and it is not suitable to simulate stand-level processes.

To evaluate climate change impacts on the forest ecosystem and its feedback, Canadian forest resources managers need a hybrid model for forest management planning. TRIPLEX (Peng et al, 2002) is a hybrid model to understand quantitatively the consequences of forest management for stand characters, especially for sustainable yield and carbon, nitrogen and water dynamics. This model has a monthly time step

and was developed from three well-established process models: 3-PG (tree growth model) (Landsberg and Waring, 1997), TREEDYN3.0 (forest growth and yield model) (Bossel, 1996), and CENTURY (soil biogeochemistry model) (Parton et al., 1993). It is comprehensive, but it is not complicated, by concentrating on the major mechanistic processes in the forest ecosystem in order to reduce some parameters. Also, this model has been tested in central and eastern Canada using traditional forest inventories (e.g., height, DBH and volume) (Peng et al, 2002; Zhou et al, 2004).

1.2.2. Model application for management practices

1.2.2.1. Species composition:

Using chronosequence analyses in central Siberia (Roser et al, 2002) and central Canda (Bond-Lamberty et al, 2005), the previous studies showed that the boreal mixedwood forest sequestrated less carbon than single species forest. However, using species-specific allometric models, Martin et al. (2005) indicated the net primary production (NPP) in the mixedwood forest was two times greater than in the single species forest, which contradicts with the previous two studies. Unfortunately, in these studies, the detailed physiological process and the effects on carbon flux of meteorological characteristics were not clear for the mixedwood forest, and most current carbon models have only focused on pure stands. Therefore, there is an immediate need to incorporate the mixedwood forest component into forest carbon dynamics models.

1.2.2.2. Thinning and harvesting

Forest management practices (such as thinning and harvesting) have had significant influence on carbon conservation of forest ecosystems, through changes in species composition, density and age structure (IPCC 1995, 1996). Currently, thinning and harvesting are two dominant management practices used in forest ecosystems (Davis et al. 2000). Intensive forest management practices based on short rotations and high levels of biomass utilization (e.g. whole-tree harvesting (WTH)) may significantly reduce forest site productivity, soil organic matter (SOM), and carbon budgets. Forest thinning is considered as an effective way to accelerate tree growth, reduce mortality and increase productivity and biomass production (Smith et al., 1997; Nabuurs et al.,

2008). On the other hand, there is a need to modify current management practices to optimize forest growth and carbon (C) sequestration under a changing environment conditions (Nuutinen et al., 2006; Garcia-Gonzalo et al., 2007). To move from conceptual to practical application of forest carbon management, there remains an urgent need to better understand how managerial activities regulate the cycling and sequestration of carbon. In the absence of long-term field trials, a process-based hybrid model (such as TRIPLEX) may provide an alternative means of examining the long-term effects of management on carbon dynamics of future Canadian boreal ecosystems. Consequently, this change requires that forest resource managers make use of forest simulation models in order to make long-term decisions (Peng, 2000).

1.3. HYPOTHESIS

In this study, I will test three critical hypotheses using a modeling approach:

(1) Given spatial and temporal heterogeneities, some sensitive parameters should be variable across different times and regions.

(2) The mixedwood boreal forest will sequestrate more carbon than single species forests.

(3) Thinning and lengthening harvest rotations would be beneficial to adjust the density and enhance the capacity of boreal forests for carbon sequestration.

1.4. GENERAL OBJECTIVES

The overall objective of this study is to simulate and analyze carbon dynamics and its balance in Canadian boreal ecosystems by developing a new version of TRIPLEX-Flux model. To reach this goal, I have undertaken the following main tasks.

TASK 1: To develop a new version of the TRIPLEX model.

So far, the big-leaf approach is utilized in the TRIPLEX model, which treats the whole canopy as a single leaf to estimate carbon fluxes (e.g., Sellers et al. 1996; Bonan, 1996). Since this single big-leaf model does not account for differences in the radiation absorbed by leaf classes (sunlit and shaded leaf), it will inevitably lead to estimation bias of carbon fluxes (Wang and Leuning, 1998), a two-leaf model will be developed to calculate gross primary productivity (GPP) in this study (Fig. 1.2).

In the old version of the TRIPLEX model, net primary productivity (NPP) is estimated by a constant parameter to proportionally allocate the GPP (Peng et al. 2002). In this study, maintenance respiration (Rm) and growth respiration (Rg) in different plant components (leaf, stem and root) will be estimated respectively for model development (Kimball et al, 1997; Chen et al, 1999).

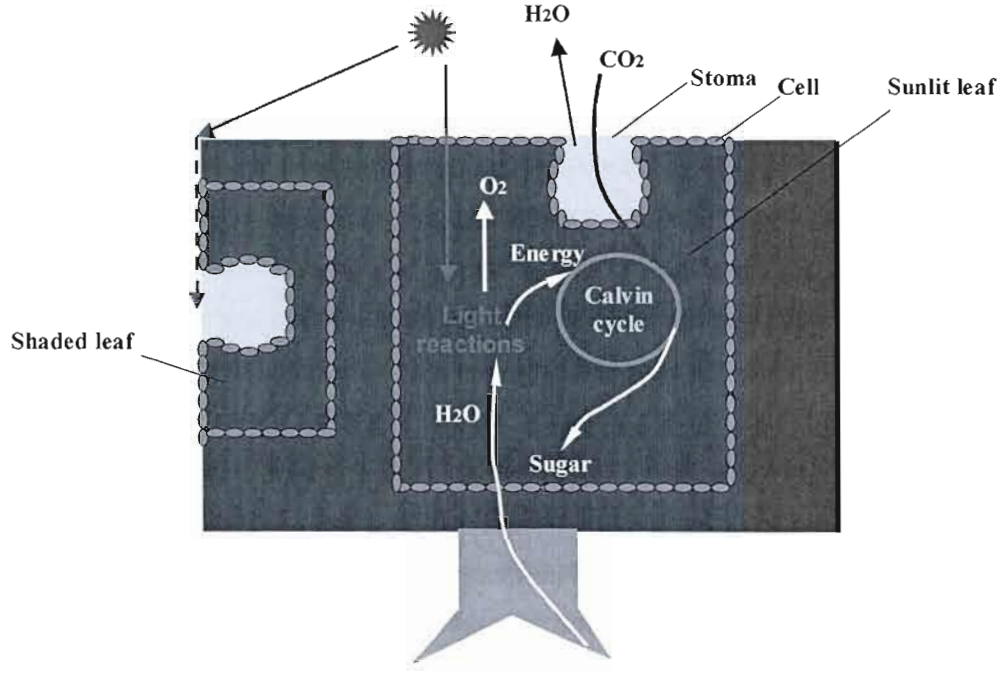

Fig. 1.2. Photosynthesis simulation of a two-leaf model.

TASK 2: To reduce modeling uncertainty of parameters estimation.

Since spatial and temporal heterogeneities within terrestrial ecosystems may lead to prediction uncertainties in models, some sensitive key parameters will be estimated by data assimilation techniques to reduce simulation uncertainties.

TASK 3: To understand the effects of species composition on carbon exchange.
In the context of boreal mixedwood forest management, an important issue for carbon sequestration and cycling is whether management practices should encourage retention of mixedwood stands or convert stands to hardwoods. To better understand the impacts of forest management on boreal mixedwoods and their carbon sequestration, it is necessary to use and develop process-based simulation models that can simulate carbon exchange between forest ecosystems and the atmosphere for different forest stands over time. Carbon fluxes will then be compared between a boreal mixedwood stand and a single species stand.

TASK 4: To understand the effects of forest thinning and harvesting on carbon sequestration.
A stand density management diagram (SDMD) will be developed to quantitatively demonstrate relationships between stand densities and stand volume and aboveground biomass at various stand developmental stages in order to determine optimal density management regimes for volume yield and for carbon storage. As well, through long-term simulation, an optimal harvesting age will be determined to uptake maximum carbon before clear cutting.

1.5. SPECIFIC OBJECTIVES AND THESIS ORGANISATION

This thesis is a combination of four manuscripts dealing with the TRIPLEX-Flux model development, validation and application. Chapter II will focus on TRIPLEX-Flux model development. In Chapter III and IV, the TRIPLEX-Flux model will be validated against observations from different forest ecosystems in Canada and North

America. This model will be applied to forest management practices in Chapter V. The relationship between these studies is showed in Fig. 1.3.

In Chapter II, the major objectives are: (1) to describe the new TRIPLEX-Flux model structure and features and to test model simulations against flux tower measurements; and (2) to examine and quantify the effects of modeling response to parameters, input variables and algorithms of the intercellular CO_2 concentrations and stomatal conductance calculations on ecosystem carbon flux. Analyses will have significant implications for the evaluation of factors that relate to gross primary productivity (GPP) as well as those that influence the outputs of a carbon flux model coupled with a two-leaf photosynthetic model.

In Chapter III, the TRIPLEX-Flux model is used to address the following three questions: (1) Are the diurnal patterns of half-hourly carbon flux in summer different between old mixedwood (OMW) and old black spruce (OBS) forest stands? (2) Does OMW sequester more carbon than OBS in the summer? Pursuant to this question, the differences of carbon fluxes (including GEP, NPP, and NEE) between these two types of forest ecosystems are explored for different months. Finally, (3) what is the relationship between NEE and the important meteorological drivers?

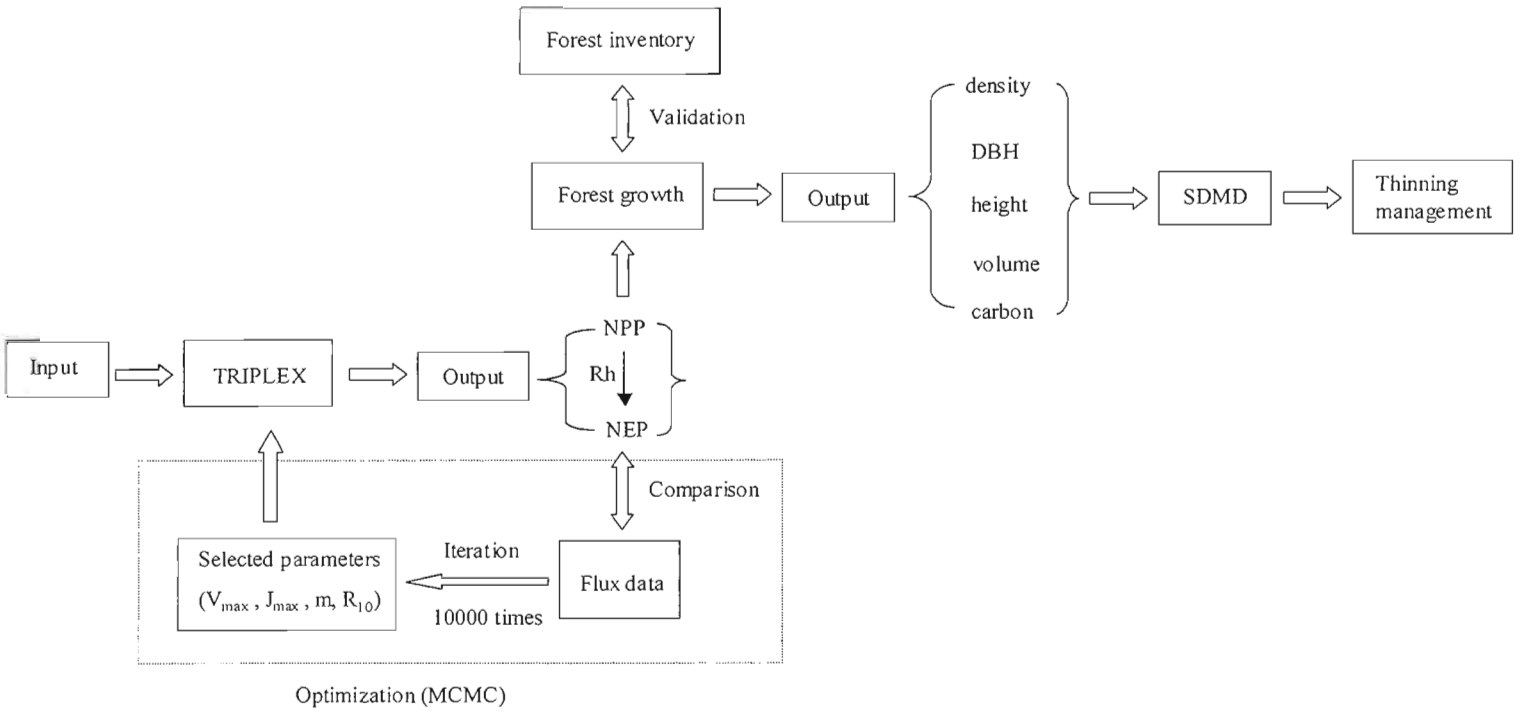

Fig. 1.3. Schematic diagram of the TRIPLEX model development, validation, optimization, and application for forest management practices.

In Chapter IV, the major objectives were (1) to test TRIPLEX-Flux model simulation against flux tower measurements taken at sites containing different tree species within Canada and the United States of America; (2) to estimate certain key parameters sensitive to environmental factors by way of flux data assimilation; and (3) to understand ecosystem productivity spatial heterogeneity by quantifying the parameters for different forest ecosystems.

In Chapter V, TRIPLEX-Flux was specifically used to investigate the following three questions: (1) is there a difference between the maturity age of a conventional forest managed for volume and the optimum rotation age at which to attain the maximum carbon storage capacity? (2) If different, how much more or less time is required to reach maximum carbon sequestration? Finally, (3) what is the realtionship between stand density and carbon storage with regards to various forest developmental stages? If all three questions can be answered with confidence then maximum carbon storage capacity should be able to be attained by thinning and harvesting in a rational and sustainable manner.

Finally, in Chapter VI, the previous Chapters' results and conclusions are integrated and synthesized. Some restrictions, limitations and uncertainties of this thesis work are summarized and discussed. The ongoing challenges and suggested directions for the future research are presented and highlighted.

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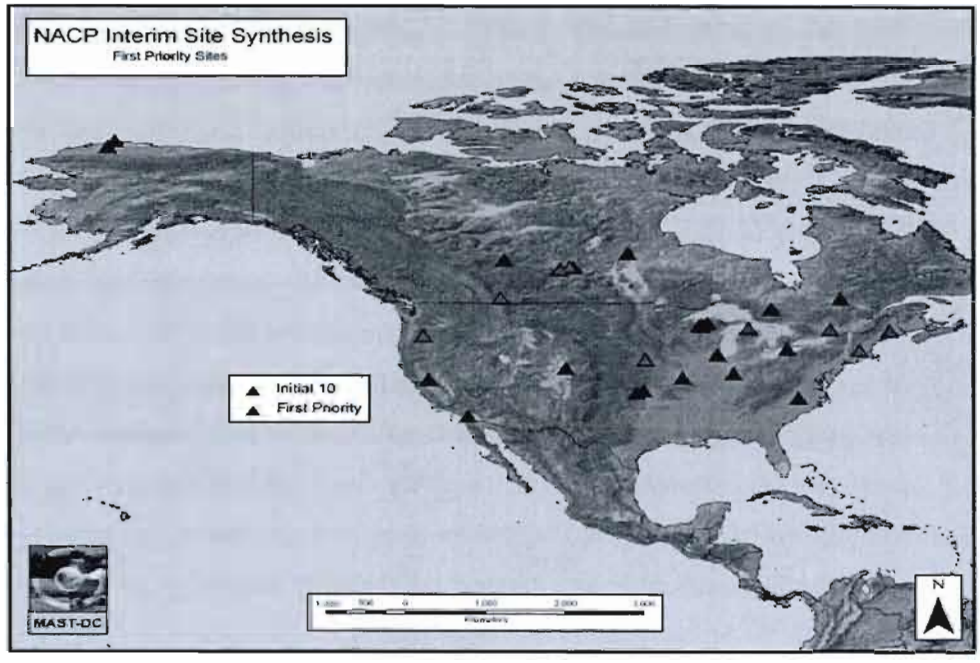

Fig. 1.4. Study sites (from Davis et al, 2008, AGU).

Table 1.1. Basic information for all study sites

Full Name	State / Province	Latitude(° N) / Longitude(° W)	Forest type	Age	AMT (°C)	AMP (mm)
BOREAS - Old Black Spruce	MB (CA)	55.88 / 98.48	ENB	160	-3.2	536
Groundhog River – Mixedwood	ON (CA)	48.22 / 82.16	MW	75	2	278
Chibougamau - Mature Black Spruce	QC (CA)	49.69 / 74.34	ENB	100	0	961
Campbell River – Mature Douglas-fir	BC (CA)	49.87 / 125.33	ENT	60	8.3	1461
BERMS – Old Aspen	SK (CA)	53.63 / 106.20	DB	83	0.4	467
BERMS – Old Black Spruce	SK (CA)	53.99 / 105.12	ENB	111	0.4	467
Harvard Forest – EMS Tower	MA (USA)	42.54 / 72.17	DB	81	8.3	1120
Howland Forest – Main Tower	ME (USA)	45.20 / 68.74	ENT	109	6.7	778
Metolius – Intermediate-aged Ponderosa Pine	OR (USA)	44.45 / 121.56	ENT	90	6.4	447
University of Michigan Biological Station	MI (USA)	45.56 / 84.71	DB	90	6.2	750

Note: MW = Mixedwood, ENB = Evergreen needleleaf boreal forest, ENT = evergreen needleleaf temperate forest, DB = broadleaf deciduous forest. Adapt from CCP and NACP.

1.6. STUDY AREA

This study was carried out at ten forest flux sites that were selected from 36 primary sites (Fig. 1.4) possessing complete data sets within the NACP Interim Synthesis: Site-Level. Information concerning these ten forest sites is presented in Table 1.1. The study area consists of three evergreen needleleaf temperate forests (ENT), three deciduous broadleaf forests (DB), three evergreen needleleaf boreal forest (ENB) and one mixedwood boreal forest spread out across Canada and the United States of America from western to eastern coast. The dominant species includes black spruce, aspen, Douglas-fir, Ponderosa Pine, Hemlock, red spruce and so on. The lines of latitude are from 42.5 ° N to 55.9° N. These forest ecosystems are located within different climatic regions with varied annual mean temperatures (AMT) ranging from – 3.2°C to 8.3°C and annual mean precipitation (AMP) ranging from 278mm to 1461mm. The age span of these forest ecosystems ranges from 60 to 160 years old and falls within the category of middle and old aged forests, respectively.

Eddy covariance flux data, climate variables (temperature, relative humidity, and wind speed), and radiation above the canopy were recorded at the flux tower sites. Gap-filled and smoothed leaf area index (LAI) data products were accessed from the MODIS website (http://accweb.nascom.nasa.gov/) for each site under the Site-Level Synthesis of the NACP Project (Schwalm et al., in press), which contains the summary statistics for each eight day period. Before NACP Project, LAI data were collected by other Fluxnet – Canada groups (at the University of Toronto and Queen's University) (Chen et al, 1997; Thomas et al, 2006).

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CHAPTER II

SIMULATING CARBON EXCHANGE OF CANADIAN BOREAL FORESTS I. MODEL STRUCTURE, VALIDATION, AND SENSITIVITY ANALYSIS

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2.1. RÉSUMÉ

Cet article présente un modèle basé sur les processus afin d'estimer la productivité nette d'un écosystème (PNE) ainsi qu'une analyse de la sensibilité de réponse du modèle lors de la simulation du flux de CO_2 sur des sites d'épinettes noires agées de BOREAS. L'objectif de la recherche était d'étudier les effets des paramètres ainsi que ceux des données entrantes sur la réponse du modèle. La validation du modèle, utilisant des données de PNE à des intervalles de 30 minutes sur des tours et des chambres de mesures, a montré que la PNE modelisée était en accord avec la PNE mesurée (R^2>0.65). L'analyse de la sensibilité a mis en évidence différentes sensibilités entre le matin et le milieu de journée, ainsi qu'entre une concentration habituelle et une concentration doublée de CO_2. De plus, la comparaison de différents algorithmes pour calculer la conductance stomatale a montré que la modélisation de la PNE, utilisant un algorithme itératif est conforme avec les résultats utilisant des rapports Ci/Ca constants de 0.74 et de 0.81 respectivement pour les concentrations courantes et doublées de CO_2. Une variation des paramètres et des données entrantes de plus ou moins 10% a entraîné une réponse du modèle inférieure ou égale à 27.6% et à 27.4% respectivement pour les concentrations courantes et doublées de CO_2. La plupart des paramètres sont plus sensibles en milieu de journée qu'au matin excepté pour ceux en lien avec la température de l'air, ce qui suggère que la température a des effets considérables sur la sensibilité du modèle pour ces paramètres/variables. L'effet de la température de l'air était plus important pour une atmosphère dont la concentration de CO_2 était doublée. Par contre, la sensibilité du modèle au CO_2 diminuait lorsque la concentration de CO_2 était doublée.

2.2. ABSTRACT

This paper presents a process-based model for estimating net ecosystem productivity (NEP) and the sensitivity analysis of model response by simulating CO_2 flux in old black spruce site in the BOREAS project. The objective of the research was to examine the effects of parameters and input variables on model responses. The validation using 30-minute interval data of NEP derived from tower and chamber measurements showed that the modelled NEP had a good agreement with the measured NEP (R^2>0.65). The sensitivity analysis demonstrated different sensitivities between morning and noonday, and from the current to doubled atmospheric CO_2 concentration. Additionally, the comparison of different algorithms for calculating stomatal conductance shows that the modeled NEP using the iteration algorithm is consistent with the results using a constant C_i/C_a of 0.74 and 0.81, respectively for the current and doubled CO_2 concentration. Varying parameter and input variable values by ±10% resulted in the model response to less and equal than 27.6% and 27.4%, respectively. Most parameters are more sensitive at noonday than in the morning except for those that are correlated with air temperature suggesting that air temperature has considerable effects on the model sensitivity to these parameters/variables. The air temperature effect was greater under doubled than current atmospheric CO_2 concentration. In contrast, the model sensitivity to CO_2 decreased under doubled CO_2 concentration.

Keywords: CO_2 flux, ecological model, TRIPLEX-FLUX, photosynthetic model, BOREAS

2.3. INTRODUCTION

Photosynthesis models play a key role for simulating carbon flux and estimating net ecosystem productivity (NEP) in studies of the terrestrial biosphere and CO_2 exchange between vegetated land surface and the atmosphere (Sellers et al, 1997; Amthor et al., 2001; Hanson et al, 2004; Grant et al. 2005). The models represent not only our primary method for integrating small-scale, process level phenomena into a comprehensive description of forest ecosystem structure and function but also a key method for testing our hypotheses about the response of forest ecosystems to changing environmental conditions. The CO_2 flux of an ecosystem is directly influenced by its photosynthetic capacity and respiration, the former is commonly simulated using mechanistic models and the latter is calculated using empirical functions to derive NEP. Since the late 1970s, a number of mechanistic-based models have been developed and used for simulating photosynthesis and respiration, and for providing a consistent description of carbon exchange between plants and environment (Sellers et al. 1997). For most models, the calculation of photosynthesis for individual leaves is theoretically based on (1) the biochemical formulations presented by Farquhar et al. (1980), and (2) the numerical solutions developed by Collatz et al. (1991). At the canopy level, the approaches of scaling up from leaf to canopy using Farquhar's model can be categorized into two types: "big-leaf" and "two-leaf" models (Sellers et al. 1996). The "two-leaf" treatment separates a canopy into sunlit and shaded portions (Kim and Verma, 1991; Norman, 1993; de Pure and Farquhar 1997), and vertical integration against radiation gradient (Bonan, 1995).

Following these pioneers' works, many studies have successfully demonstrated the application of process-based carbon exchange models by improving model structure and parameterizing models for different ecosystems (Tiktak, 1995; Amthor et al., 2001; Hanson et al, 2004; Grant et al. 2005). For example, BEPS-InTEC (Liu et al, 1997; Chen et al. 1999), CLASS (Verseghy, 2000), ECOSYS (Grant, 2001), C-CLASSa (Wang et al, 2001), C-CLASSm (Arain et al, 2002), EALCO (Wang et al, 2002), and CTEM (Arora et al, 2003) are the principle process-based models used in the Fluxnet-Canada Research Network (FCRN) for modeling NEP at hourly or daily

time steps. However, these derivative and improved models usually require a large number of parameters and input variables that in practice are difficult to obtain and estimate for characterizing various forest stands and soil properties (Grant et al, 2005). This complexity of model results is a difficulty for modelers to perceptively understand model responses to such a large number of parameters and variables. Although many model parameterizations responsible for the simulation biases were diagnosed and corrected by the individual site, it is still unclear how to resolve the differences among parameterizations for different sites and climate conditions. Additionally, different algorithms for intermediate variables in a model usually affect model accuracy. For example, there are various considerations and approaches to process the intercellular CO_2 concentration (C_i) for calculating instantaneous CO_2 exchange. This key variable C_i is derived in various ways: (1) using empirical constant ratio of C_i to the atmospheric CO_2 concentration (C_a); (2) as a function of relative humidity, atmospheric CO_2 concentration, and a species-specific constant (Kirschbaum, 1999) by eliminating stomatal conductance; (3) using a nested numerical convergence technique to find an optimized C_i, which meets the canopy energy balance of CO_2 and water exchange for a time point (Leuning, 1990; Collatz et al., 1991; Sellers et al., 1996; Baldocchi and Meyers, 1998). These approaches can significantly affect the accuracy and efficiency of a model. The effects of different algorithms on NEP estimation are of great concern in model selection that influences both the accuracy and efficiency of the model.

Moreover, fluctuations in photosynthetic rate are highly correlated with the daily cycle of radiation and temperature. These cyclic ups and downs of photosynthetic rate can be well captured using process-based carbon flux models (Amthor et al., 2001; Grant et al., 2005) and neural network approach by training for several daily cycles (Papale and Valentini, 2003). However, the CO_2 flux is often underestimated during the day and overestimated at night, even though the frequency of alternation and diurnal cycle are simulated accurately. Amthor et al. (2001) compared nine process-based models for evaluating model accuracy, and found those models covered a wide range of complexity and approaches for simulating ecosystem processes. Modelled annual CO_2 exchange was more variable between models within a year than between years for a

given model. This means that differences between the models and their parameterizations are more important to the prediction of CO_2 exchange than the interannual climatic variability. Grant et al. (2005) tested six ecosystem models for simulating the effects of air temperature and vapor pressure deficit (VPD) on carbon balance. They suggested that the underestimation of net carbon gain was attributed to an inadequate sensitivity of stomatal conductance to VPD and of eco-respiration to temperature in some models. Their results imply the need and challenge to improve the ability of CO_2 flux simulation models on NEP estimation by recognizing how the structure and parameters of a model will influence model output and accuracy. Aber (1997) and Hanson et al (2004) suggested that prior to the application of a given model for the purpose of simulation and prediction, appropriate documentation of the model structure, parameterization process, sensitivity analysis, and testing of model output against independent observation must be conducted.

To improve the parameterization schemes in the development of ecosystem carbon flux models, we performed a series of sensitivity analyses using the new canopy photosynthetic model of TRIPLEX-FLUX, which is developed for simulating carbon exchange in Canada's boreal forest ecosystems. The major objective of this study was to examine and quantify the effects of model responses to parameters, input variables, and algorithms of the intercellular CO_2 concentration and stomatal conductance calculations on ecosystem carbon flux. The analyses have significant implications on the evaluation of factors that relate to GPP and influence the outputs of a carbon flux model coupled with a two-leaf photosynthetic model. The results of this study suggest sensitive indices for model parameters and variables, estimate possible variations in model response resulted by changing parameters and variables, and present references on model tests for simulating the carbon flux of black spruce in boreal forest ecosystems.

2.4. MATERIALS AND METHODS

2.4.1. Model development and description

2.4.1.1. Model structure

TRIPLEX-FLUX is designed to take advantage of the approach used in the two-leaf mechanistic model to describe the irradiance and photosynthesis of the canopy, and to simulate CO_2 flux of boreal forest ecosystems. The model consists of three parts: (1) leaf photosynthesis: The instantaneous gross photosynthetic rate is derived based on the biochemical model of Farquhar et al. (1980) and the semi-analytical approach of Collatz et al. (1991), which simulates photosynthesis using the concept of co-limitation by Rubisco (V_c) and electron transport (V_j). (2) Canopy photosynthesis: total canopy photosynthesis is simulated using de Pury and Farquhar's algorithm in which a canopy is divided into sunlit and shaded portions. The model describes the dynamics of abiotic variables, such as radiation, irradiation, and diffusion. (3) Ecosystem carbon flux: the net ecosystem exchange (NEP) is modeled as the difference between photosynthetic carbon uptake and respiratory carbon loss (including autotrophic and heterotrophic respiration) that is calculated using Q_{10} and a base temperature.

Fig. 2.1 illustrates the primary processes and output of the model, and control mechanisms. All parameters and their default values, and variables and functions for calculating them are listed in Table 2.1. The A_{canopy} is the sum of photosynthesis in the shaded and sunlit portion of the crowns, depending on the outcome of V_c and V_j (see Table 2.1). The A_{c_sunlit} and A_{c_shade} are net CO_2 assimilation rates for sunlit and shaded leaves in the canopy.

The model runs at 30 minutes time steps, and outputs carbon flux at different time intervals.

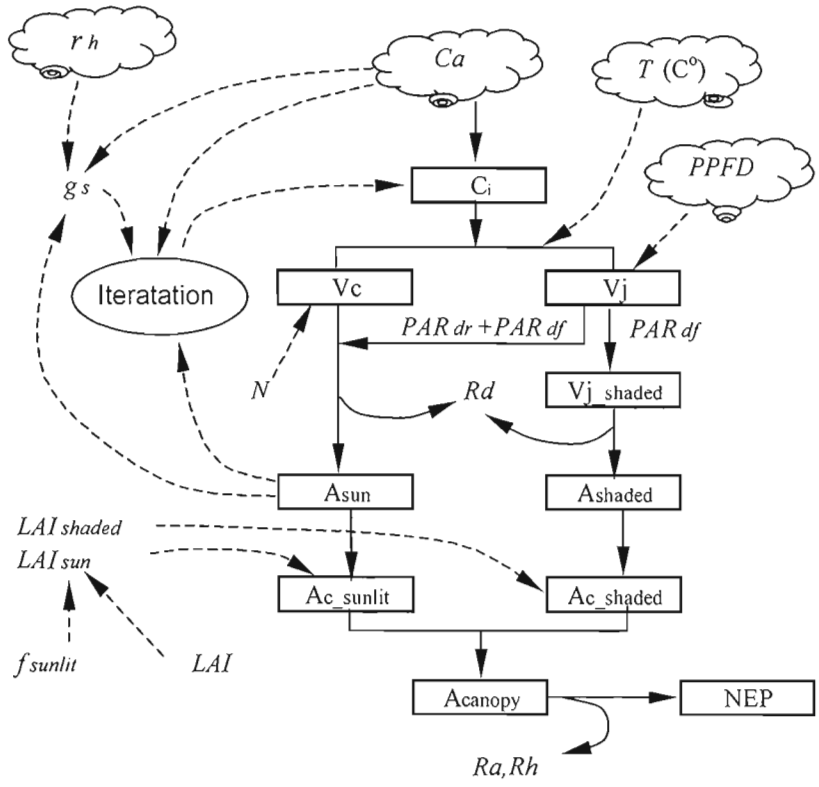

Fig. 2.1. The model structure of TRIPLEX-FLUX. Rectangles represent key pools or state variables, and ovals represent simulation process. Solid lines represent carbon flows and the fluxes between the forest ecosystem and external environment, and dashed lines denote control and effects of environmental variables. The A_{canopy} represents the sum of photosynthesis in the shaded and sunlit portion of the crowns, depending on the outcome of V_c and V_j (see Table 1). The A_{c_sunlit} and A_{c_shade} are net CO_2 assimilation rates for sunlit and shaded leaves; the f_{sunlit} denotes the fraction of sunlit leaf of the canopy.

Table 2.1. Variables and parameters used in TRIPLEX-FLUX for simulating old black spruce of boreal forest in Canada.

Symbol	Unit	Description	Equation and Value	Reference
A	mol m^{-2} s^{-1}	net CO_2 assimilation rate for big leaf	$A = \min(V_c, V_j) - Rd$ $A = g_s(C_a-C_i)/1.6$	Farquhar et al. (1980), Leuning (1990), Sellers et al. (1996)
A_{canopy}	mol m^{-2} s^{-1}	net CO_2 assimilation rate for canopy	$A_{canopy} = A_{sun}$ $LAI_{sun} + A_{shade}$ LAI_{shade}	Norman, (1982)
A_{shade}	mol m^{-2} s^{-1}	net CO_2 assimilation rate for shaded leaf		
A_{sun}	mol m^{-2} s^{-1}	net CO_2 assimilation rate for sunlit leaf		
Γ	Pa	CO_2 compensation point without dark respiration	$\Gamma = 1.92 * 10^{-4}$ O_2 $1.75^{(T-25)/10}$	Collatz et al. (1991) and Sellers et al. (1992)
C_a	Pa	CO_2 concentration in the atmosphere	Input variable	
C_i	Pa	intercellular CO_2 concentration		
f(N)	-	nitrogen limitation term	$f(N) = N/N_m = 0.8$	Bonan (1995)
f(T)	-	temperature limitation term	$f(T) = (1+\exp((-220{,}000 +710(T+273))/(R_{gas}$	Bonan (1995)

			$(T+273)))))^{-1}$	
g_s	m mol m^{-2} s^{-1}	stomatal conductance	$g_s = g_o + m100A\ r_h /Ca$	Ball et al. (1988)
g_o	-	initial stomatal conductance	57.34	Cai and Dang (2002)
m	-	coefficient	7.43	Cai and Dang (2002)
J	mol m^{-2} s^{-1}	electron transport rate	$J = J_{max}$ PPFD/(PPFD + 2.1 J_{max})	Farquhar and von Caemmerer (1982)
Jmax	mol m^{-2} s^{-1}	light-saturated rate of electron transport in the photosynthetic carbon reduction cycle in leaf cells	$J_{max} = 29.1 + 1.64\ V_m$	Wullschleger (1993)
K	Pa	function of enzyme kinetics	$K = K_c (1 + O_2 /$ Ko)	Collatz et al. (1991) and Sellers et al. (1992)
K_c	Pa	Michaelis–Menten constants for CO_2	$K_c = 30 * 2.1^{(T - 25)/10}$	Collatz et al. (1991) and Sellers et al. (1992)
K_o	Pa	Michaelis–Menten constants for O_2	$K_o = 30000 * 1.2^{(T - 25)/10}$	Collatz et al. (1991)
M	kg C m^{-2} day^{-1}	biomass density of each plant component	0.4 for leaf 0.28 for sapwood 1.4 for root	Gower et al. (1977) Kimball et al.

				(1997) Steel et al. (1997)
N	%	leaf nitrogen content	1.2	Based on Kimball et al. (1997)
N_m	%	maximum nitrogen content.	1.5	Bonan (1995)
O_2	Pa	oxygen concentration in the atmosphere,	21,000	Chen et al. (1999)
PPFD	mol m^{-2} s^{-1}	photosynthetic photon flux density	Input variable	
Q_{10}	-	temperature sensitivity factor	2.0	Goulden et al. (1997)
R_a	kg C m^{-2} day^{-1}	autotrophic respiration	$R_a = R_m + R_g$	
r_a	-	carbon allocation fraction	0.4 for root 0.6 for leaf and sapwood	Running and Coughlan (1988)
R_d	mol m^{-2} s^{-1}	leaf dark respiration	$R_d = 0.015V_m$	Collatz et al. (1991)
R_e	kg C m^{-2} day^{-1}	ecosystem respiration	$R_e = R_a + R_h$	
R_g	kg C m^{-2} day^{-1}	growth respiration	$R_g = r_g r_a$ GPP	Ryan (1991)
r_g	-	growth respiration coefficient	0.25 for root, leaf and sapwood	Ryan (1991)
R_{gas}	m^3 Pa mol^{-1} K^{-1}	molar gas constant	8.3143	Chen et al., 1999

r_h	%	relative humidity	Input variable	
R_h	kg C m^{-2} day^{-1}	heterotrophic respiration	$R_h = 1.5\ Q_{10}^{(T-10)/10}$	Lloyd and Taylor 1994
R_m	kg C m^{-2} day^{-1}	maintenance respiration	$R_m = M\ r_m\ Q_{10}^{(T-T_o)/10}$	Running and Coughlan (1988), Ryan (1991)
r_m	-	maintenance respiration coefficient	0.002 at 20°C for leaf 0.001 at 20°C for stem 0.001 at 20°C for root	Kimball et al. (1997)
T	°C	air temperature	Input variable	
V_c	mol m^{-2} s^{-1}	Rubisco-limited gross photosynthesis rates	$V_c = V_m (C_i - \Gamma)/(C_i - K)$	Farquhar et al. (1980)
V_j	mol m^{-2} s^{-1}	Light-limited gross photosynthesis rates	$V_j = J (C_i - \Gamma)/(4.5C_i + 10.5\Gamma)$	Farquhar and von Caemmerer (1982)
V_m	mol m^{-2} s^{-1}	maximum carboxylation rate	$V_m = V_{m25}\ 0.24\ (T - 25)\ f(T)\ f(N)$	Bonan (1995)
V_{m25}	mol m^{-2} s^{-1}	V_m at 25°C, variable depending on vegetation type	45	Depending on Cai and Dang (2002)

2.4.1.2. Leaf photosynthesis

The instantaneous leaf gross photosynthesis was calculated using Farquhar's model (Farquhar et al., 1980 and 1982). The model simulation consists of two components: Rubisco-limited gross photosynthetic rate (V_c) and light-limited (RuBP or electron transportation limited) gross photosynthesis rate (V_j), which are expressed for C_3 plants as shown in Table 1. The minimum of the two are considered as the gross photosynthetic rate of the leaf without considering the sink limitation to CO_2 assimilation. The net CO_2 assimilation rate (A) is calculated by subtracting the leaf dark respiration (Rd) from the above photosynthetic rate:

$$A = \min(V_c, V_j) - Rd \quad [1]$$

This can also be further expressed using stomatal conductance and the difference of CO_2 concentration (Leuning, 1990):

$$A = g_s(C_a - C_i)/1.6 \quad [2]$$

Stomatal conductance can be derived in several different ways. We used the semi-empirical g_s model developed by Ball et al. (1988):

$$g_s = g_o + 100mA\, r_h/C_a \quad [3]$$

All symbols in Equation [1], [2], and [3] are described in Table 1.Because the intercellular CO_2 concentration C_i (Equations [1] and [2]) has a nonlinear response on the assimilation rate A, full analytical solutions cannot be obtained for hourly simulations. The iteration approach is used in this study to obtain C_i and A using Equation [1], [2], and [3] (Leuning, 1990; Collatz et al., 1991; Sellers et al., 1996; Baldocchi and Meyers, 1998). To simplify the algorithm, we did not use the conservation equation for water transfer through stomata. Stomatal conductance was calculated using a simple regression equation (R^2=0.7) developed by Cai and Dang (2000) based on their experiments on black spruce:

$$g_s = 57.4 + 743A\, r_h/C_a \quad [4]$$

2.4.1.3. Canopy photosynthesis

In this study, we coupled the one-layer and two-leaf model to scale up the photosynthesis model from leaf to canopy, and assumed that sunlit leaves receive direct PAR (PAR_{dir}) while shaded leaves receive diffusive PAR (PAR_{dif}) only.

Assuming the mean leaf-sun angle to be 60° for a boreal forest canopy with spherical leaf angle distribution, the PAR received by sunlit leaves includes PAR_{dir} and PAR_{dif}, while the PAR for shaded leaves is only PAR_{dif}. Norman (1982) proposed an approach to calculate direct and diffusive radiations, which can be used to run the numerical solution procedure (Leuning, 1990; Collatz et al., 1991; Sellers et al., 1996) for obtaining the net assimilation rate of sunlit and shaded leaves (A_{sun} and A_{shade}). With the separation of sunlit and shaded leaf groups, the total canopy photosynthesis (A_{canopy}) is obtained as follows (Norman, 1981, 1993; de Pure and Farquhar, 1997):

$$A_{canopy} = A_{sun}\, LAI_{sun} + A_{shade}\, LAI_{shade} \qquad [5]$$

where LAI_{sun} and LAI_{shade} are the leaf area index for sun leaf and shade leaf, respectively; the calculation for LAI_{sun} and LAI_{shade} is described by Pure and Farquhar (1997)

2.4.1.4. Ecosystem carbon flux

Net Ecosystem Production (NEP) is estimated by subtracting ecosystem respiration (Re) from GPP (A_{canopy}):

$$NEP = GPP - Re \qquad [6]$$

where $R_e = R_g + R_m + R_h$. Growth respiration (R_g) is calculated based on respiration coefficients and GPP, and maintenance respiration (R_m) is calculated using the Q_{10} function multiplied by the biomass of each plant component. Both R_g and R_m are calculated separately for leaf, sapwood, and root carbon allocation fractions:

$$\mathbf{R_g = \Sigma\, (r_g\, r_a\, GPP)} \qquad [7]$$

$$\mathbf{R_m = \Sigma\, (M\, r_m\, Q_{10}^{(T-To)/10})} \qquad [8]$$

where r_g, r_a, r_m and M represent adjusting coefficients and the biomass for leaf, root, and sapwood, respectively (see Table 1). The heterotrophic respiration (R_h) is calculated using an empirical function of temperature (Lloyd and Taylor, 1994)

2.4.2. Experimental data

The tower flux data used for model testing and comparison were collected at old black spruce (*Picea mariana* (Mill.) BSP) site in the Northern Study Area (FLX-01 NSA-OBS) of BOREAS (Nickeson et al., 2002). The trees at the upland site were average 160 years-old and 10 m tall in 1993 (see Table 2.2). The site contained poorly drained silt and clay, and 10% fen within 500 m of the tower (Chen et al., 1999). Further details about the sites and the measurements can be found in Sellers et al. (1997). The data used as model input include CO_2 concentration in the atmosphere, air temperature, relative humidity, and photosynthetic photon flux density (PPFD). The 30-minute NEP derived from tower and chamber measures was compared with model output (NEP).

Table 2.2. Site characteristics and stand variables.

Site	BOREAS-NOBS: Northern Study Area, Old Black Spruce, Flux Tower, Manitoba, Canada
Latitude	55.88° N
Longitude	98.48° W
Mean January air temperature (°C)	-25.0
Mean July air temperature (°C)	+15.7
Mean annual precipitation (mm)	536
Dominant species	black spruce *Picea mariana* (Mill.)
Average stand age (years)	160
Average height (m)	10.0
Leaf area index (LAI)	4.0

2.5. RESULTS AND DISCUSSION

2.5.1. Model validation

Model validation was performed using the NEP data measured in May, July, and September of 1994-1997 at the old black spruce site of BOREAS. The simulated data were compared with observed NEP measurements at 30-minute intervals for the month of July from 1994 to 1997 (Fig. 2.2). The simulated NEP and measured NEP is the one-to-one relationship (Fig. 2.3) with a R^2>0.65. The relatively good agreement between observations and predictions suggests that the parameterization of the model was consistent by contributing to realistic predictions. The patterns of NEP simulated by the model (solid line as shown in Fig. 2.2) matches most observations (dots as shown in Fig. 2.2). However, the TRIPLEX-FLUX model failed to simulate some peaks and valleys of NEP. For example, biases occur particularly at 5th, 7th, 9th, 10th, and 11th July 1994 (peaks) and 8th, 13th, 14th, 21st, and 22nd in July 1994 (valleys). The difference between model simulation and observations can be attributed not only to the uncertainties and errors of flux tower measurement (Grant et al, 2005; also see the companion paper of Sun et al in this issue) but also to the model itself.

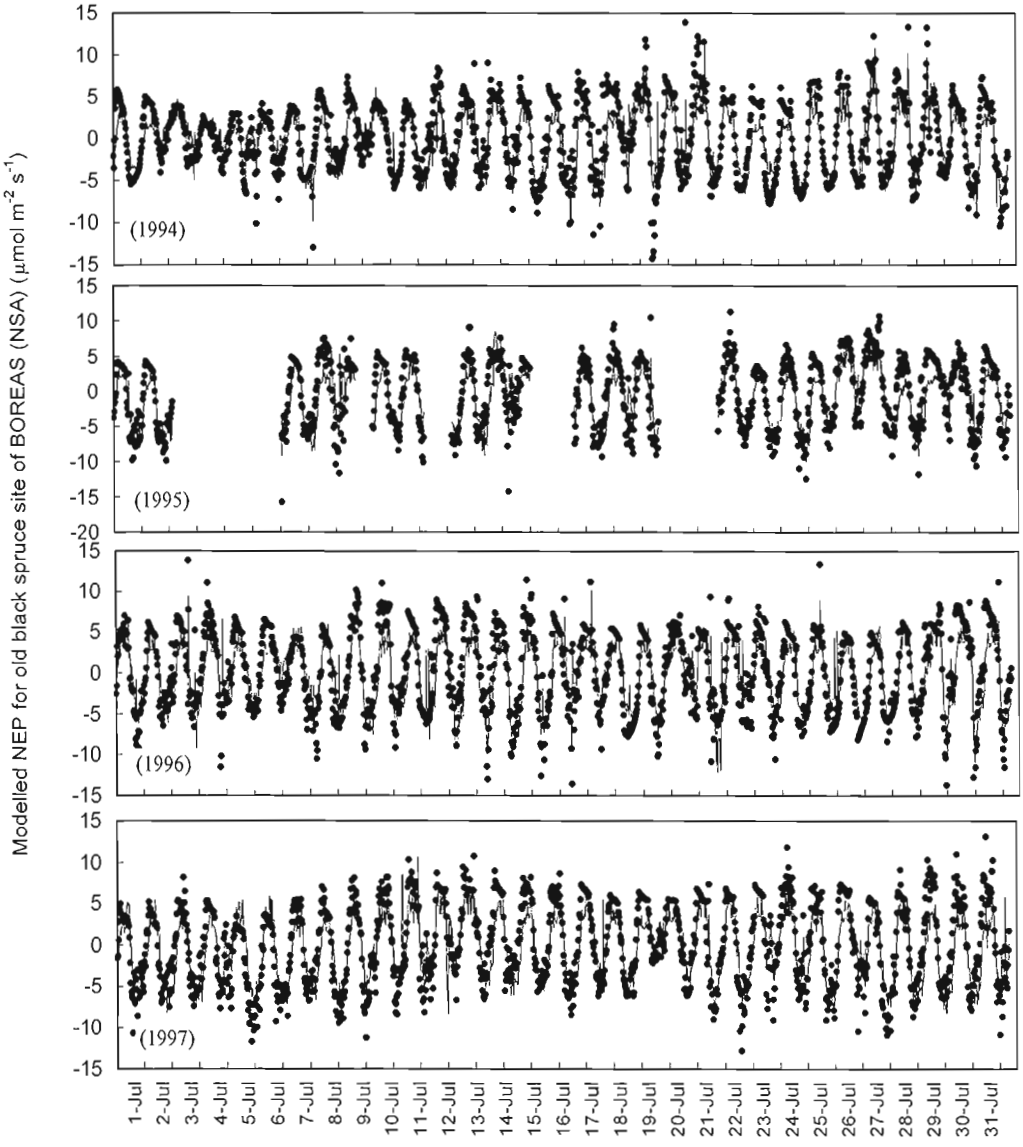

Fig. 2.2. The contrast of hourly simulated NEP by the TRIPLEX-FLUX and observed NEP from tower and chamber at old black spruce BOREAS site for July in 1994, 1995, 1996, and 1997. Solid dots denote measured NEP and solid line represents simulated NEP. The discontinuances of dots and lines present the missing measurements of NEP and associated climate variables.

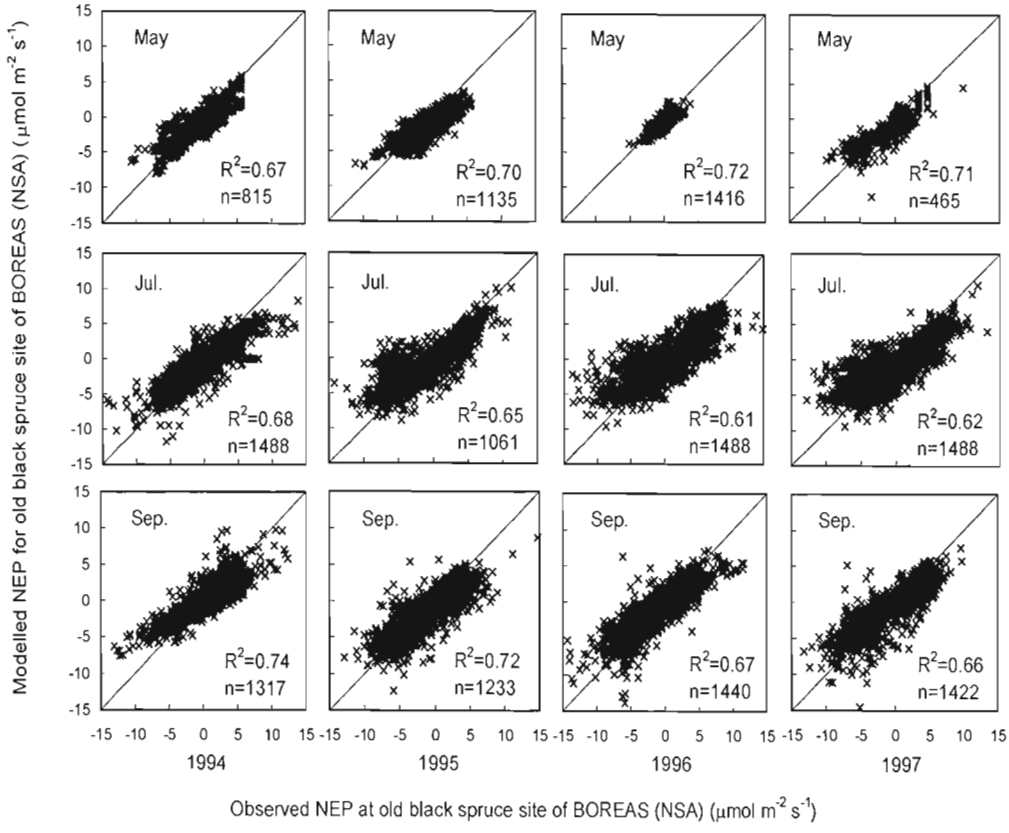

Fig. 2.3. Comparisons (with 1:1 line) of hourly simulated NEP vs hourly observed NEP for May, July, and September in 1994, 1995, 1996, and 1997.

Because NEP is determined by both GPP and ecosystem respiration (Re), it is necessary to verify the modeled GEP. Since the real GEP could not be measured for that site, we compared modeled GEP with the GEE derived from observed NEE and Re (Fig. 2.4). The confections of determination (R^2) are higher than 0.67 for July in each observation year (from 1994 to 1997). This implied that the model structure and parameters are correctly set up for this site.

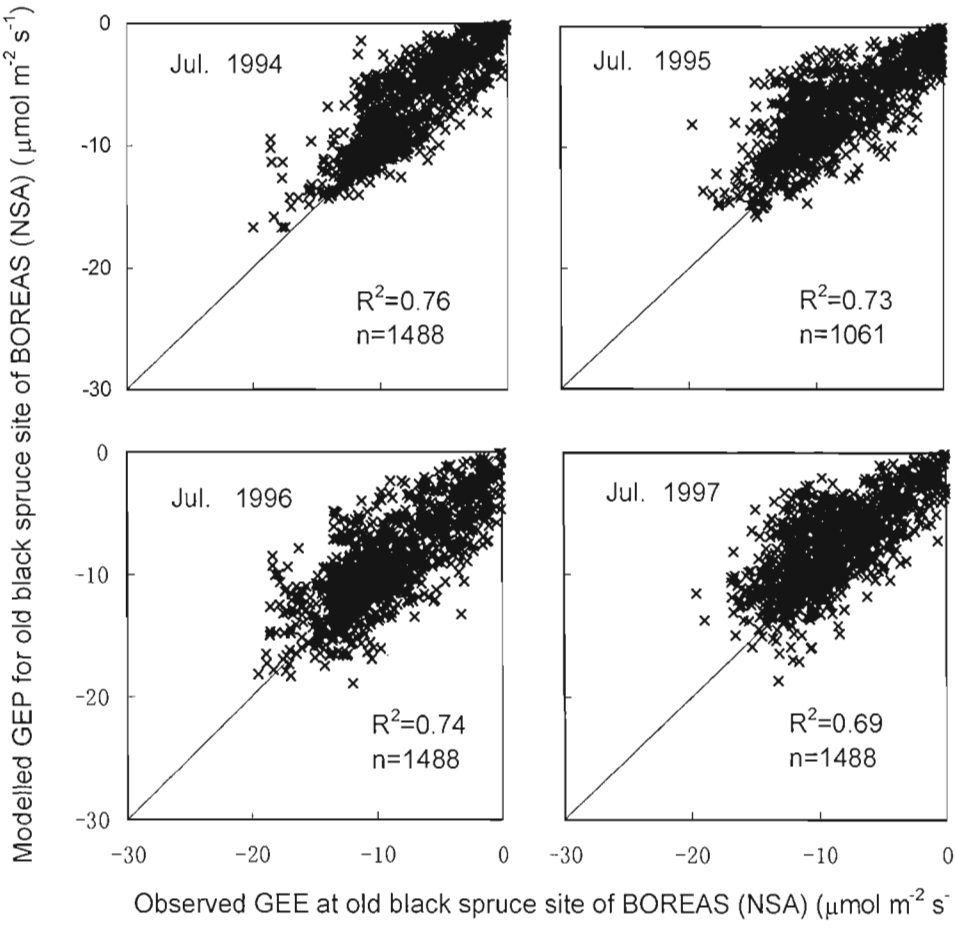

Fig. 2.4. Comparisons of hourly simulated GEP vs hourly observed GEP for July in 1994, 1995, 1996, and 1997.

From a modeling point of view, the bias usually results from two possible causes: one is that the inconsequential model structure cannot take into account short-term changes in the environment, and another is that the variation in the environment is out of the modelling limitation. To identify the reason for the bias in this study, we compared variations of simulated NEP values for all time steps with similar environmental conditions, such as the atmospheric CO_2 concentration, air temperature, relative humidity, and photosynthetic photon flux density (PPFD). Unfortunately, the comparison failed to pinpoint the causes for the biases, since similar environmental conditions may drive estimated NEP significantly higher or lower than the average

simulated by the model. This implies that the CO_2 flux model may need more input environmental variables than the four key variables used in our simulations. For example, soil temperature may cause the respiration change and influence the amount of ecosystem respiration and the partition between root and heterotrophic respirations. The empirical function (Equation [3]) does not describe the relationship of soil respiration with other environmental variables other than air temperature. Additionally, soil water potential could also influence simulated stomatal conductance (Tuzet et al., 2003), which may result in lower assimilation under soil drought despite more irradiation available (Xu et al., 2004). These are some of the factors that need to be considered in the future versions of the TIPLEX-FLUX model. The further testing and application of TRIPLEX-FLUX for other boreal tree species at different locations can be found in the companion paper of Sun et al, in this issue).

2.5.2. Sensitivity analysis

The sensitivity analysis was conducted under two different climate conditions that are based on the current atmospheric CO_2 concentration and doubled CO_2 concentration. Additionally, the model sensitivity was tested and analyzed for morning and noon. The four selected variables of model inputs (lower Ca, T, r_h, and PPFD) are the averaged values at 9:00 and 13:00 h, respectively. The higher Ca was set up at 720 ppm and the air temperature was adjusted based on the CGCM scenario that air temperature will increase up to approximately 3 °C at the end of 21st century. Table 2.3 presents the various scenarios of model run in the sensitivity analysis, and modeled values for providing reference levels.

Table 2.3. The model inputs and responses used as the reference level in model sensitivity analysis. LAI_{sun} and LAI_{sh} represent leaf area index for sunlit and shaded leaf; $PPFD_{sun}$ and $PPFD_{sh}$ denote the photosynthetic photon flux density for sunlit and shaded leaf. Morning and noon denote the time at 9:00 and 13:00.

		C_a=360		C_a=720		Unit
		Morning	Noon	Morning	Noon	
Input:						
	C_a	360	360	720	720	ppm
	T	15	25	15	25	°C
	r_h	64.	64	64	64	%
	PPFD	680	1300	680	1300	mol m^{-2} s^{-1}
Modelled:						
	NEP	0.14	0.22	0.19	0.34	g C m^{-2} $30min^{-1}$
	R_e	0.13	0.17	0.16	0.32	g C m^{-2} $30min^{-1}$
	LAI_{sh}/LAI_{sun}	0.56	1.44	0.56	1.44	-
	$PPFD_{sh}/PPFD_{sun}$	0.25	0.23	0.25	0.23	-

Table 2.4. Effects of parameters and inputs to model response of NEP. Morning and noon denote the time at 9:00 and 13:00.

			C_a=360		C_a=720	
			Morning	Noon	Morning	Noon
Parameters	f(N)	+10%	8.7%	11.9%	4.9%	8.4%
		-10%	-14.5%	-15.7%	-8.6%	-10.3%
	Q_{10}	+10%	3.4%	-2.8%	1.4%	-1.7%
		-10%	-3.4%	2.7%	-1.4%	1.7%
	r_{in}	+10%	-7.0%	-5.8%	-4.1%	-3.6%
		-10%	0.9%	5.2%	1.4%	3.3%
	r_g	+10%	-5.9%	-6.4%	-5.6%	-5.3%
		-10%	5.5%	5.7%	4.4%	4.8%
	r_a	+10%	<0.1%	<0.1%	<0.1%	<0.1%
		-10%	<0.1%	<0.1%	<0.1%	<0.1%
	a	+10%	-1.2%	-0.3%	-0.9%	-0.5%
		-10%	1.2%	0.3%	0.9%	0.5%
	b	+10%	-1.6%	-1.7%	-1.1%	-1.1%
		-10%	1.6%	1.7%	1.2%	1.1%
	g_o	+10%	0.3%	<0.1%	<0.1%	<0.1%
		-10%	<0.1%	<0.1%	<0.1%	<0.1%
	m	+10%	<0.1%	<0.1%	<0.1%	<0.1%
		-10%	<0.1%	<0.1%	<0.1%	<0.1%
Inputs	C_a	+10%	7.4%	12.7%	1.9%	3.0%
		-10%	-9.9%	-14.7%	-2.4%	-4.0%
	T	+10%	2.6%	-8.3%	2.4%	3.5%
		-10%	-3.3%	1.2%	-2.4%	-6.2%
	r_h	+10%	2.4%	<0.1%	0.5%	0.6%
		-10%	-2.6%	<0.1%	-0.6%	-0.7%
	PPFD	+10%	1.0%	0.8%	2.4%	2.3%
		-10%	-1.2%	-1.0%	-3.0%	-2.8%

Table 2.5. Sensitivity indices for the dependence of the modelled NEP on the selected model parameters and inputs. Morning and noon denote the time at 9:00 and 13:00. The sensitivity indices were calculated as ratios of the change (in percentage) of model response to the given baseline of 20%.

	C_a=360		C_a=720		Average
	Morning	Noon	Morning	Noon	
Parameters					
f(N)	1.16	1.38	0.68	0.93	1.04
r_g	0.57	0.60	0.50	0.50	0.54
r_m	0.39	0.55	0.28	0.35	0.39
Q_{10}	0.34	0.27	0.14	0.17	0.23
b	0.16	0.17	0.11	0.11	0.14
a	0.12	<0.1	<0.1	<0.1	<0.1
g_o	<0.1	<0.1	<0.1	<0.1	<0.1
m	<0.1	<0.1	<0.1	<0.1	<0.1
r_a	<0.1	<0.1	<0.1	<0.1	<0.1
Inputs					
C_a	0.90	1.38	0.22	0.35	0.37
T	0.35	0.48	0.24	0.49	0.25
PPFD	0.33	<0.1	0.27	0.26	0.19
r_h	0.33	<0.1	0.14	<0.1	0.13

2.5.3. Parameter testing

Nine parameters were selected from the parameters listed in Table 2.1 for the model sensitivity analysis. Because the parameters vary considerably depending upon forest conditions, it is difficult to determine them for different tree ages, sites, and locations. These selected parameters are believed to be critical for the prediction accuracy of a CO_2 flux model, which is based on a coupled photosynthesis model for simulating

stomatal conductance, maximum carboxylation rate, and autotrophic and heterotrophic respirations. Table 2.4 summarizes the results of the model sensitivity analysis and Table 2.5 presents suggested sensitive indices for model parameters and input variables. Each parameter in Table 2.4 was altered separately by increasing or and decreasing its value by 10 %. The sensitivity of model output (NEP) is expressed as a percentage change.

The modeled NEP varied directly with the proportion of nitrogen limitation (f(N)), and changed in directly or inversely to Q_{10} depending on the time of the day (i.e., morning or noon) because the base temperature (20°C) was between the morning temperature (15°C) and noon (solar noon, i.e. 13:00 in the summer) temperature (25°C) (Table 3). The NEP varied inversely with changes in parameters with the exception of r_a, g_o and m, which had little effects on model output (NEP). The response of model output to ±10% changes in parameter values was less than 27.6% and generally greater under the current than under doubled atmospheric CO_2 concentration (Fig. 2.5). The simulation showed that increased CO_2 concentration reduces the model sensitivity to parameters. Therefore, CO_2 concentration should be considered as a key factor modeling NEP because it affects the sensitivity of the model to parameters. Fig. 2.5 shows that the model is very sensitive to f(N), indicating greater efforts should be made to improve the accuracy of f(N) in order to increase the prediction accuracy of the NEP using the TRIPLEX-FLUX model.

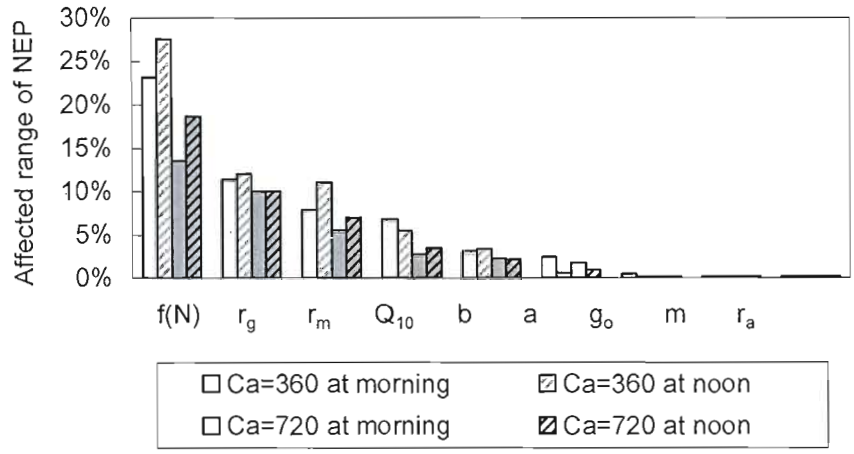

Fig. 2.5. Variations of modelled NEP affected by each parameter as shown in Table 4. Morning and noon denote the time at 9:00 and 13:00.

2.5.4. Model input variable testing

Generally speaking, the model response to input variables is of great significance in the model development phase because in this phase the response can be compared with other results to determine the reliability of the model. We tested the sensitivity of the TRIPLEX-FLUX model to all input variables. Under the current atmospheric CO_2 concentration, C_a had larger effects than other input variables on the model output. By changing ±10% values of input variables, the modeled NEP varied from 17.3% to 27.6% under temperatures 15°C (morning) and 25°C (noon) (Table 2.4 and Figure 2.6). A 10% increase in the atmospheric CO_2 concentration at noon only increased the model output of NEP by 7%. In contrast to the greater impact of parameters, the effect of air temperature on NEP was smaller under the current than under doubled CO_2 concentration. This may be related the suppression of photorespiration by increased CO_2 concentration. Thus, air temperature may be a highly sensitive input variable at high atmospheric CO_2 concentrations. However, the current version of our model does not consider photosynthetic acclimation to CO_2 (down- or up-regulation) whether the temperature impact will change when photosynthetic acclimation occurs warrants further investigation.

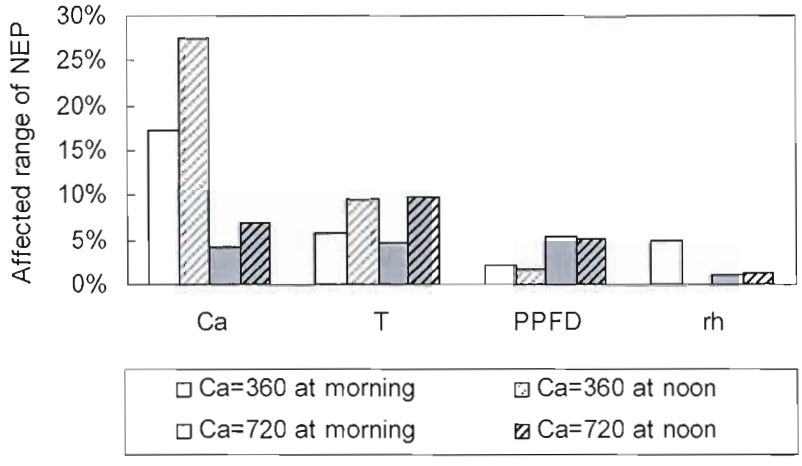

Fig. 2.6. Variations of modelled NEP affected by each model input as listed in Table 4. Morning and noon denote the time at 9:00 and 13:00.

Fig. 2.7. is the temperature response curve of modelled NEP, which shows that the sensitivity of the model output to temperature changes with the range of temperature. The curves peaked at 20°C under the current C_a and at 25°C under doubled C_a. The modelled NEP increased by about 57% from current C_a at 20°C to doubled C_a at 25°C. The C_a sensitivity is close to the value (increased by about 60%) reported by McMurtrie and Wang (1993).

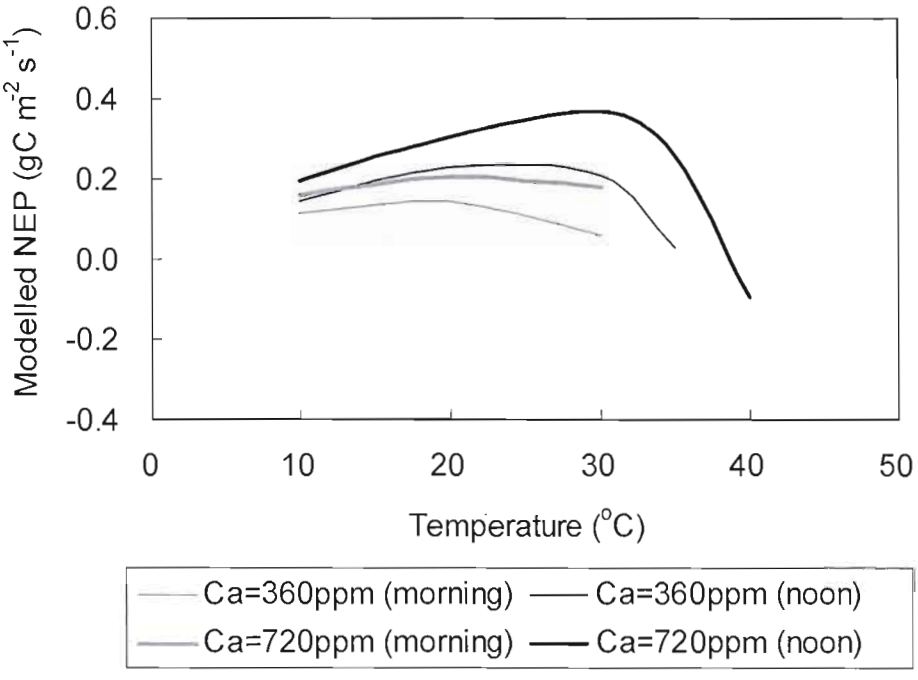

Fig. 2.7. The temperature dependence of modelled NEP. Solid line denotes doubled CO_2 concentration, and dashed line represents current air CO_2 concentration. The four curves represent different simulating conditions: current CO_2 concentration in the morning (regular gray line) and noonday (bold gray line), and doubled CO_2 concentration in the morning (regular black line) and at noon (bold black line). Morning and noon denote the time at 9:00 and 13:00.

The effects of C_a and air temperature on NEP are more than those of PPFD and relative humidity (r_h). In addition, C_a can also govern effects of r_h as different between morning and noon. For example, r_h affects NEP more in the morning than at noon under current CO_2 concentration (C_a=360ppm). Figure 5 shows 6.1% variation of NEP in the morning and less than 0.1% at noon, which suggests no strong relationship between stomatal opening and r_h at noon. It is because the stomata opens at noon to reach a maximal stomatal conductance, which can be estimated as 300mmol m^{-2} s^{-1} according to Cai and Dang's experiment (2002) of stomatal conductance for boreal forests. In contrast, doubled CO_2 (C_a=720ppm) results in effects of r_h were always above 0%

(Figure 5). This implies that the stomata may not completely open at noontime because an increasing CO_2 concentration leads to a significant decline of stomatal conductance, which reduces approximately 30% of stomatal conductance under doubled CO_2 concentration (Morison, 1987 and 2001; Wullschleger et al., 2001; Talbott, et al., 2003).

2.5.5. Stomatal CO_2 flux algorithm testing

The sensitivity analysis performed in this study included the examination of different algorithms for calculating intercellular CO_2 concentration (C_i). Because stomatal conductance determines C_i at a given C_a, different algorithms of stomatal conductance affect C_i values and thus the modelled NEP for the ecosystem. To simplify the algorithm, Wong et al. (1979) performed a set of experiments that suggest that C_3 plants tend to keep the C_i/C_a ratio constant. We compared model responses to two algorithms of C_i, i.e., the iteration algorithm and the ratio of C_i to C_a. The iteration algorithm resulted in a variation in the C_i/C_a ratio from 0.73 to 0.82 (Figure 8). The C_i/C_a was lower in the morning than at noontime, and higher under doubled than current CO_2 concentration. This range of variation agrees with Baldocchi's results which showed C_i/C_a ranging from 0.65 to 0.9 with modeled stomatal conductance ranging from 20 to 300 mmol m^{-2} s^{-1} (Baldocchi, 1994), but our values are slightly greater than Wong's experimental value of 0.7 (Wong et al. 1979). Our results suggest that a constant ratio (C_i/C_a) may not express realistic dynamics of the C_i/C_a ratio as if primarily depends on air temperature and relative humidity.

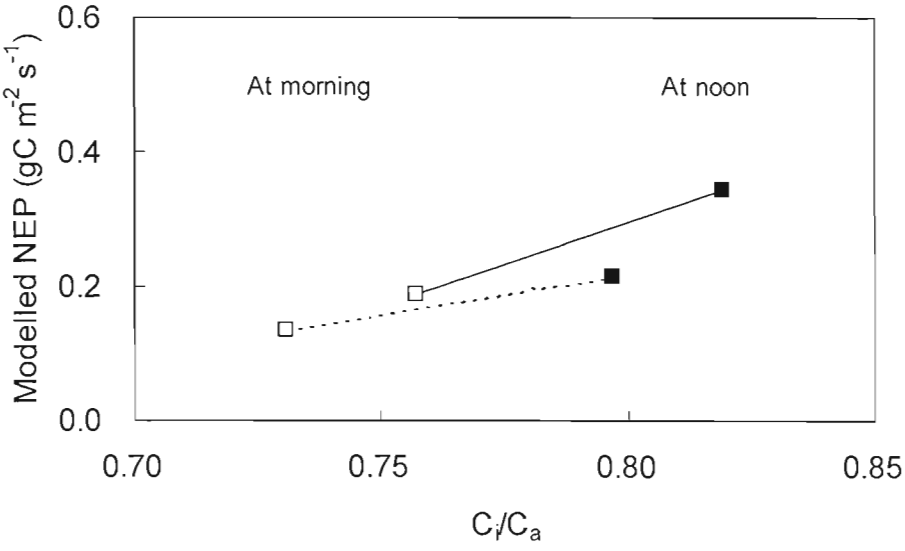

Fig. 2.8. The responses of NEP simulation using coupling the iteration approach to the proportions of C_i/C_a under different CO_2 concentrations and timing. Open and solid squares denote morning and noon; dashed and solid lines represent current CO_2 and doubled CO_2 concentration, respectively. Morning and noon denote the times at 9:00 and 13:00.

Generally speaking, stomatal conductance is affected by five environmental variables: solar radiation, air temperature, humidity, atmospheric CO_2 concentration, and soil water potential. The stomatal conductance model (iteration algorithm) used in this study does not consider the effect of soil water, unfortunately. The Ball-Berry model (Ball et al. (1988) requires only A, r_h and C_a as input variables, however, some investigations have argued that stomatal conductance is dependent on water vapor pressure deficit (Aphalo and Jarvis, 1991; Leuning, 1995), and transpiration (Mott and Parkhurst, 1991; Monteith, 1995), rather than r_h, especially under dry environmental conditions (de Pury, 1995).

By coupling the regression function (Equation [3]) of stomatal conductance with leaf photosynthesis model, we did not find that g_o and m described in Equation [3] affect NEP significantly. Although the stomatal conductance is critical for governing the

exchanges of CO_2 and water, the initial stomatal conductance (g_o) does not affect the stomatal conductance (g_s) a lot if we use Ball's model. It implies that stomatal conductance (g_s) relative mainly with A, r_h, and Ca other than g_o and m. These two parameters suggested for black spruce in northwest Ontario (Cai and Dabg, 2002) can be applied to the wider BOREAS region. We notice that Ball's model does not address some variables to simulate the stomatal conductance (g_s), for example, soil water. To improve the model structure, the algorithm affecting model response needs to be considered for further testing the sensitivity of stomatal conductance by describing effects of soil water potential for simulating NEP of boreal forest ecosystem. Several models have been reported as having the ability to relate stomatal conductance to soil moisture. For example, Jarvis's model (Jarvis, 1976) contains a multiplicative function of photosynthetic active radiation, temperature, humidity deficits, molecular diffusivity, soil moisture, and carbon dioxide; the Mäkelä model (Mäkelä et al., 1996) has a function for photosynthesis and evaporation; and the ABA model (Triboulot et al., 1996) has a function for leaf water potential. These models comprehensively consider major factors affecting stomatal conductance. Nevertheless, it is worth noting that changing the algorithm for stomatal conductance will impact the model structure. Because there is no feedback between stomatal conductance and internal CO_2 in the algorithm, it is debatable whether Jarvis' model is appropriate to be coupled into an iterative model.

2.6. CONCLUSION

We described the development and general structure of a simple process-based carbon exchange model TRIPLEX-FLUX, which is based on well-tested representations of ecophysiological processes and a two-leaf mechanistic modeling approach. The model validation suggests that the TRIPLEX-FLUX is able to capture the diurnal variations and patterns of NEP for old black spruce in central Canada, but failed to simulate the peaks in NEP during the1994-1997 growing seasons. The sensitivity analysis carried out in this study is critical for understanding the relative roles of different model parameters in determining the dynamics of net ecosystem productivity. The nitrogen factor had the highest effect on modeled NEP (causing 27.6% variation at noon), the

autotrophic respiration coefficients have intermediate sensitivity, and others are relatively low in terms of the model response. The parameters used in the stomatal conductance function were not found to affect model response significantly. This raised an issue, which should be clarified in future modeling work. Model inputs are also examined for the sensitivity to model output. Modelled NEP is more sensitive to the atmospheric CO_2 concentration, resulting in 27.4% variation of NEP at noon and followed by air temperature (e.g., 9.5% at noon) then the photosynthetic photon flux density and relative humidity. The simulations showed different sensitivities in the morning and at noon. Most parameters were more sensitive at noon than in the morning except those related to air temperature, such as Q_{10} and coefficients for the regression function of soil respiration. The results suggest that air temperature had considerable effects on the sensitivity of these temperature-dependent parameters. Under the assumption of doubled CO_2 concentration, the sensitivities of modelled NEP decreased for all parameters and increased for most model input variables except atmospheric CO_2 concentration. It implies that temperature related factors are crucial and more sensitive than other factors used in modelling ecosystem NEP when atmospheric CO_2 concentration increases. Additionally, the model validation suggests that more input variables than the current four used in this study are necessary to improve model performance and prediction accuracy.

2.7. ACKNOWLEDGEMENTS

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CHAPTER III

SIMULATING CARBON EXCHANGE OF CANADIAN BOREAL FORESTS II. COMPARING THE CARBON BUDGETS OF A BOREAL MIXEDWOOD STAND TO A BLACK SPRUCE STAND

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3.1. RÉSUMÉ

La forêt boréale, second biome terrestre en importance, est actuellement considerée comme un puits important de carbone pour l'atmosphère. Dans cette étude, un modèle nouvellement développé d'échange du carbone, TRIPLEX-Flux (avec des étapes d'une demi-heure), est utilisé pour simuler l'échange de carbone des écosystèmes d'un peuplement forestier mixte boréal de 75 ans du Nord-Est de l'Ontario et d'un peuplement d'épinette noire de 110 ans du Sud de la Saskatchewan au Canada. Les résultats de l'échange net de l'écosystème (ENE) simulé par TRIPLEX-Flux sur l'année 2004 sont comparés à ceux mesurés par les tours de mesures des flux turbulents et montrent une correspondance générale entre les simulations du modèle et les observations de terrain. Le coefficient de détermination moyen (R^2) est approximativement de 0.77 pour le peuplement mixte boréal et de 0.62 pour le peuplement d'épinette noire. Les différences entre les simulations du modèle et les observations du terrain peuvent être attribuées à des incertitudes qui ne seraient pas uniquement dues aux paramètres du modèle et à leur calibrage, mais également à des erreurs systématique et aléatoires des mesures des tours de turbulence. Le modèle est capable d'intégrer les variations diurnes de la période de croissance (de mai a août) de 2004 sur les deux sites. Le peuplement boréal mixte ainsi que le peuplement d'épinette noire agissaient tous deux comme puits de carbone pour l'atmosphère durant la période de croissance de 2004. Cependant le peuplement boréal mixte montre une plus grande productivité de l'écosystème, un plus grand piégeage du carbone ainsi qu'un meilleur taux de carbone utilisé comparativement au peuplement d'épinette noire.

3.2. ABSTRACT

The boreal forest, Earth's second largest terrestrial biome, is currently thought to be an important net carbon sink for the atmosphere. In this study, a newly developed carbon exchange model of TRIPLEX-Flux (with half-hourly time step) is used to simulate the ecosystem carbon exchange of a 75-year-old boreal mixedwood forest stand in northeast Ontario and a 110-year-old pure black spruce stand in southern Saskatchewan, Canada. Results of net ecosystem exchange (NEE) simulated by TRIPLEX-Flux for 2004 are compared with those measured by eddy flux towers and suggest overall agreement between model simulation and observations. The mean coefficient of determination (R^2) is approximately 0.77 for boreal mixedwood and 0.62 for old black spruce. Differences between model simulation and observations may be attributed to uncertainties not only in model input parameters and calibration, but also in eddy-flux measurements caused by systematic and random errors. The model is able to capture the diurnal variations of NEE for the growing season (from May to August) of 2004 for both sites. Both boreal mixedwood and old black spruce were acting as carbon sinks for the atmosphere during the growing season of 2004. However, the boreal mixedwood stand shows higher ecosystem productivity, carbon sequestration, and carbon use efficiency than the old black spruce stand.

Keywords: net ecosystem production, TRIPLEX-Flux model, eddy covariance, model validation, carbon sequestration

3.3. INTRODUCTION

Boreal forests form Earth's second largest terrestrial biome and play a significant role in the global carbon cycle, because boreal forests are currently thought to be important net carbon sinks for the atmosphere (D'Arrigo et al., 1987; Tans et al., 1990; Ciais et al., 1995; Sellers et al., 1997; Fan et al., 1998; Gower et al, 2001; Bond-Lamberty et al., 2004; Dunn et al., 2007). Canadian boreal forests account for about 25% of global boreal forest and nearly 90% of productive forest area in Canada. Mixedwood forest, defined as mixtures of two or more tree species dominating the forest canopy, is a common, productive, and economically important forest type in Canadian boreal ecosystems (Chen et al., 2002). In Ontario, mixedwood stands occupy approximately 46% of the boreal forest area (Towill et al. 2000). In the context of boreal mixedwood forest management, an important issue for carbon sequestration and cycling is whether management practices should encourage retention of mixedwood stands or conversion to conifers. To better understand the impacts of forest management on boreal mixedwoods and their carbon sequestration, it is necessary to use and develop process-based simulation models that can simulate carbon exchange between forest ecosystems and atmosphere for different forest stands over time. However, most current carbon models have only focused on pure stands (Carey et al., 2001; Bond-Lamberty et al., 2005) and very few studies have been carried out to investigate carbon budgets for boreal mixedwoods in Canada (Wang et al., 1995; Sellers et al., 1997; Martin et al., 2005)

Whether boreal mixedwood forests sequester more carbon than single species stands is under debate. On the one hand, chronosequence analyses of boreal forests in central Siberia (Roser et al., 2002) and in central Canada (Bond-Lamberty et al., 2005) suggest that boreal mixedwood forests sequester less carbon than single-species forests. On the other hand, using species-specific allometric models and field measurements, Martin et al (2005) estimated that net primary productivity (NPP) of a mixedwood forest in central Canada was two times greater than that of the single species forest. However, in these studies, the detailed physiological processes and the effects of meteorological characteristics on carbon fluxes and stocks were not examined for boreal mixedwood

forests. The Fluxnet-Canada Research Network (FCRN) provides a unique opportunity to analyze the contributions of different boreal ecosystem components to carbon fluxes and budgets. Specifically, this research compares carbon flux simulations and observations for two of the sites within the network, a 110-year-old pure black spruce stand in Saskatchewan (OBS) and a 75-year-old boreal mixedwood stand in Ontario (OMW).

In this study, TRIPLEX-Flux (with half-hourly time steps) is used to simulate the carbon flux of the OMW and OBS. Simulated carbon budgets of the two stands and the responses of gross ecosystem productivity (GEP), ecosystem respiration (ER) and net ecosystem exchange (NEE) to diurnal climatic variability are compared to the results of eddy covariance measurements from FCRN. The overall objective of this study was to compare ecosystem responses of a pure black spruce stand and a mixedwood stand in a boreal forest ecosystem. Specifically, the model is used to address the following three questions: (1) Are the diurnal patterns of half-hourly carbon flux in summer different between OMW and OBS forest stands? (2) Does the OMW sequester more carbon than OBS in the summer? Pursuant to this question, the differences of carbon fluxes (including GEP, NPP, and NEE) between these two types of forest ecosystems are explored for different months. Finally, (3) what is the relationship between NEE and the important meteorological drivers?

3.4. METHODS

3.4.1 Sites description

The OMW and OBS sites provide continuous backbone flux and meteorological data to the FCRN web-based data information system (DIS). These data are available to network participants and collaborators for carbon flux modelling and other research efforts. Specific details about the measurements at each site are described in McCaughey et al. (this issue) and Barr et al. (this issue) for the OMW and OBS sites, respectively.

3.4.1.1. Ontario Boreal mixedwood (OMW) site

The Groundhog River Flux Station (GRFS) of Ontario (Table 1) is a typical boreal mixedwood site, located approximately 80 km southwest of Timmins, near Foleyet. Vegetation principally includes trembling aspen (*Populus tremuloides* Michx), black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss), white birch (*Betula papyrifera* Marsh) and balsam fir (*Abies balsamea* (L.) Mill). Some short herbaceous species and mosses are also found on the forest floor. The soil has a 15-cm-deep organic layer and a deep B horizon. The latter is characterized as a silty very fine sand (SivfS) which seems to have an upper layer, about 25 cm deep, tentatively identified as a Bf horizon, which overlies a deep second and lighter colored B horizon. Snow melts around mid-April (DOY 100) and leaf emergence occurs at the end of May (DOY 150).

Ten permanent National Forestry Inventory (NFI) sample plots have been established across the site. These data suggest an average basal area of 26.4 m^2/ha and an average biomass in living trees of 165.4 Mg/ha, 134.5 Mg/ha of which is contained in above-ground parts, and 30.9 Mg/ha below ground. The canopy top height is quite variable across the site in both east-west and north-south orientations, ranging from approximately 10 m to 30 m. A 41-m research tower has been established in the approximate center of a patch of forest, 2 km in diameter. The above-canopy eddy covariance flux package is deployed at the top platform of the tower at approximately 41 m for half-hourly flux measurement. Initially, from July to October 2003, the carbon dioxide flux was measured with an open-path IRGA (LI-7500). Since November 2003, the fluxes have been measured with a closed-path IRGA (LI-7000). A CO_2 profile is being measured to estimate the carbon dioxide storage term between the ground and the above-canopy flux package.

Hemispherical photographs were collected to characterize leaf area index (LAI) across the range of species associations present at OMW. Photographs were processed to extract effective plant area index (PAIe) using the digital hemispherical photography (DHP) software package and further processed to LAI using TRACwin, based on the procedures outlined and evaluated in Leblanc *et al.* (2005). Three different techniques

for calculating the clumping index were compared, including: the Lang and Xiang (1986) logarithmic method; the Chen and Chilar (1995 a,b) gap size distribution method; and the combined gap size distribution/logarithmic method. Woody-to-total area (WAI) values for the deciduous species were determined using the gap fraction calculated from leaf-off hemispherical photographs (e.g., Leblanc, 2004). Values for trembling aspen were compared to Gower et al. (1999) to ensure the validity of this approach. Average needle-to-shoot ratios for the coniferous species were calculated based on results in Gower et al. (1999) and Chen et al. (1997). The species-level LAI results were used in conjunction with species-level basal area (Thomas et al., 2006) to calculate an LAI value, which is representative of the entire site.

3.4.1.2. Old black spruce (OBS) site

The mature black spruce stand in Saskatchewan (Table 1.1) is part of the Boreal Ecosystem Research and Monitoring Sites (BERMS) project (McCaughey et al., 2000). This research site was established in 1999, following BOREAS (Sellers et al., 1997), and has run continuously since that time. The site is located near the southern edge of the current boreal forest, which has the same tree species but at a different location (old black spruce of Northern Study Area (NSA-OBS), Manitoba, Canada). At the centre of the site, a 25-m double-scaffold tower extends 5 m above the forest canopy. Soil respiration measurements have been automated since summer 2001. The soil is poorly drained peat layer over mineral substrate with some low shrubs and feather moss ground cover. Topography is gentle with a relief 550m to 730m. The field data used in this study are based on 2004 measurements and flux tower observations. Chen (1996) has used both optical instruments and destructive sampling methods to measure LAI along a 300-m transect nearby Candle Lake, Saskatchewan. The LAI was estimated to be 3.7, 4.0 and 3.9 in June, July and September, respectively.

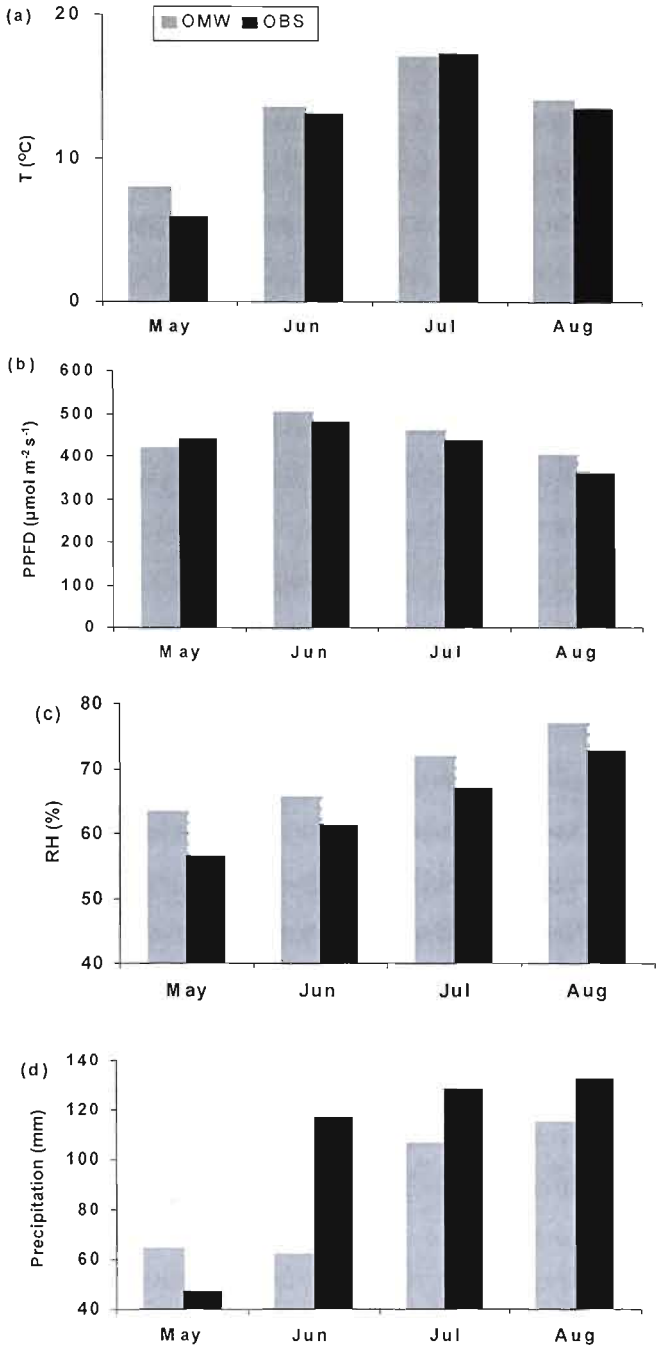

Fig. 3.1. Observations of mean monthly air temperature, PPDF, relative humidity, and precipitation during the growing season (May- August) of 2004 for both OMW and OBS.

3.4.2. Meteorological characteristics

Figure 3.1 provides the mean monthly values for air temperature, PPFD, relative humidity and precipitation from May to August of 2004 for both OMW and OBS sites. The sites have similar mean monthly air temperature and PPFD at canopy height in the summer of 2004. The air temperature was lowest in May, with value of 6°C and 8°C in OBS and OMW respectively, and highest in July with 17°C at both sites. Mean monthly PPFD was above 350 mol m^{-2} s^{-1} for the summer months and slightly higher at OMW than OBS. The relative humidity and precipitation increased over the time in both sites during these four months. The relative humidity of OMW was roughly 10% higher than OBS for each month. However, the precipitation at OMW was much less than OBS except in May (Figure 3.1).

3.4.3 Model description

The newly developed process-based TRIPLEX-Flux (Zhou et al., 2006) shares similar features with TRIPLEX (Peng et al., 2002). It is comprehensive without being complex, minimizing the number of input parameters required while capturing key well-understood mechanistic processes and important interactions among the carbon, nitrogen and water cycles of a complex forest ecosystem. The TRIPLEX-Flux adopted the two-leaf mechanistic approach (de Pury and Farquhar, 1997, Chen et al., 1999) to quantify the carbon exchange rate of the plant canopy. The model uses well-tested representations of ecophysiological processes, such as the Farquhar model of leaf-level photosynthesis (Farquhar et al., 1980, 1982) and a unique semi-empirical stomatal conductance model developed by Ball et al (1987). To scale up leaf-level photosynthesis to canopy level, the TRIPLEX-Flux coupled a one-layer and a two-leaf model of de Pury and Farquhar (1997) by calculating the net assimilation rates of sunlit and shaded leaves. A simple submodel of ecosystem respiration was integrated into the photosynthesis model to estimate NEE. The NEE is calculated as the difference between GEP and ER. The model to be operated at a half-hour time step, which allows the model to be flexible enough to resolve the interaction between microclimate and physiology at a fine temporal scale for comparison with tower flux measurements. Zhou et al. (2006) described the detailed structure and sensitivity of a new carbon

exchange model, TRIPLEX-Flux, and demonstrate its ability to simulate the carbon balance of boreal forest ecosystems.

3.4.4 Model parameters and simulations

LAI, air temperature, PPFD and relative humidity are the key driving variables for TRIPEX-Flux. Additional major variables and parameters that influence the magnitude of ecosystem photosynthesis and respiration, such as Vcmax (maximum carboxylation rate), Q_{10} (change in rate of a reaction in response to a 10°C change in temperature), leaf nitrogen content and growth respiration coefficient, are listed in Tables 3.1 and 3.2. The model was performed using observed half-hourly meteorological data, which were measured from May to August in 2004 at both study sites. The simulated CO_2 fluxes over the OBS and OMW canopies were compared with flux tower measurements for the 2004 growing season. The TRIPLEX-flux requires information on vegetation and physiological characteristics that are given in Tables 3.1 and 3.2. Linear regression of the observed data against the model simulation results was used to examine the model's predictive ability. Finally, the simulated total monthly GEP, NPP, NEE, autotrophic respiration (Ra) and heterotrophic respiration (Rh) were examined and compared for both OMW and OBS.

Table 3.1. Stand characteristics of boreal mixedwood (OWM) and old black spruce (OBS) forest. TA, trembling aspen; WS, white spruce; BS, black spruce; WB, white birch; BF, balsam fir.

Site	OBS (South, Saskatchewan)	OMW (Northeast, Ontario)
Latitude	53.987° N	48.21° N
Longitude	105.118° W	82.156° W
Mean annual air temperature (°C) at canopy height in 2004	0.7	2.0
Mean annual photosynthetic photon flux density. mol m^{-2} s^{-1})	274	275
Mean annual relative humidity (%)	71	74
Dominant species	BS	A, WS, BS, WB, BF
Stand age (years)	110	75
Height (m)	5-15	10-30
Tree density (tree/ha)	6120 - 8725	1225-1400

Table 3.2. Input and parameters used in TRIPLEX-Flux

Parameters	Units	OMW	OBS	Reference
Leaf area index	m^2/m^2	2-3[a]	3.7-4.0[b]	(a) Thomas et al (in press); (b) Chen, 1996
Q_{10}		2.3	2.3	Chen et al., 1999
Maximum leaf nitrogen content	%	2.5	1.5	Bonan, 1995
Leaf nitrogen content	%	2	1.2	Kimball et al., 1997
Maximum carboxylation rate at 25°C	mol m^{-2} s^{-1}	60	50	Cai and Dang, 2002
Growth respiration coefficient		0.25	0.25	Ryan, 1991
Maintenance respiration coefficient at 20°C (Root, stem, leaf)		0.002, 0.001, 0.002	0.002, 0.001, 0.002	Kimball et al., 1997
Oxygen concentration in the atmosphere	Pa	21000	21000	Chen et al., 1999

Note: (a) measurement from OMW is a species-weighted average for the entire site.

3.5. RESULTS AND DISCUSSIONS

3.5.1. Model testing and simulations

Simulations made by TRIPLEX-Flux were compared to tower flux measurements to assess the predictive ability and behaviour of the model, and identify its strengths and weaknesses. The results of comparison of NEE simulated by TRIPLEX-Flux with those observed by flux towers for both OMW and OBS suggest that model simulations are consistent with the range of independent measurements (Figure 2).

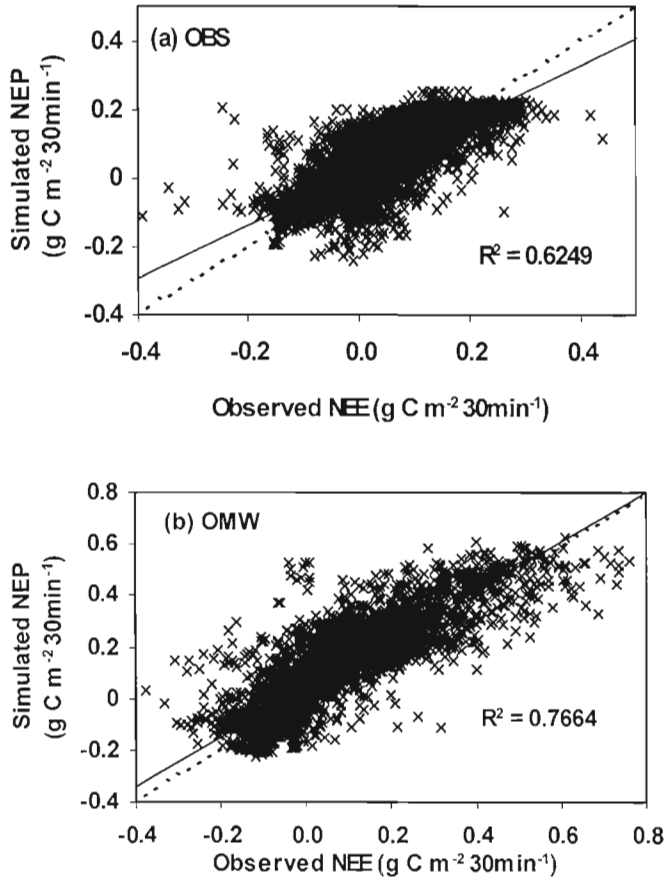

Fig. 3.2. Comparison between measured and modeled NEE for (a) old black spruce (OBS) (R^2 = 0.62, n=5904, SD =0.0605, $p<0.0001$) and Ontario boreal mixedwood (OMW) (R^2 = 0.77, n=5904, SD = 0.0819, $p<0.0001$).

Based on the mean coefficient of determination (r^2), overall agreement between model simulation and observations are reasonable (i.e., r^2 = 0.62 and 0.77 for OBS and OMW, respectively). This suggests that TRIPLEX-Flux is able to capture the diurnal variations and patterns of NEE during 2004 growing seasons for both sites, but has some difficulty simulating peaks of NEE. This result is consistent with model-measured comparisons reported for other process-based carbon exchange models (e.g., Amthor et al., 2001; Hanson et al., 2004; and Grant et al., 2005). The difference between the model and measurements can be attributed to several factors limiting

model performance: (1) model input and calibration (e.g. site and physiological parameters) are imperfectly known, and input uncertainty can propagate through the model to its outputs (Larocque et al. 2006); (2) the model itself may be biased or show unsystematic errors that can be sources of error; (3) uncertainty in eddy-flux measurements because of systematic and random errors (Wofsy et al., 1993; Goulden et al., 1996; Falge et al., 2001) caused by the underestimation of night-time respiratory fluxes and lack of energy balance closure, as well as gap-filling for missing data (Anthoni et al (1999) indicated an estimate of systematic errors in daytime CO_2 eddy-flux measurements of about $\pm$ 12%); and (4) site heterogeneity (e.g. species composition and soil texture) can play an important role in controlling NEE and causes a spatial mismatch between flux tower measurements and model simulations.

3.5.2. Diurnal variations of measured and simulated NEE

The half-hourly carbon exchange results of model simulation and observations through May to August of 2004 are presented in Figures 3 and 4. These two sites have different diurnal patterns, but the model captures the NEE variations of both sites.

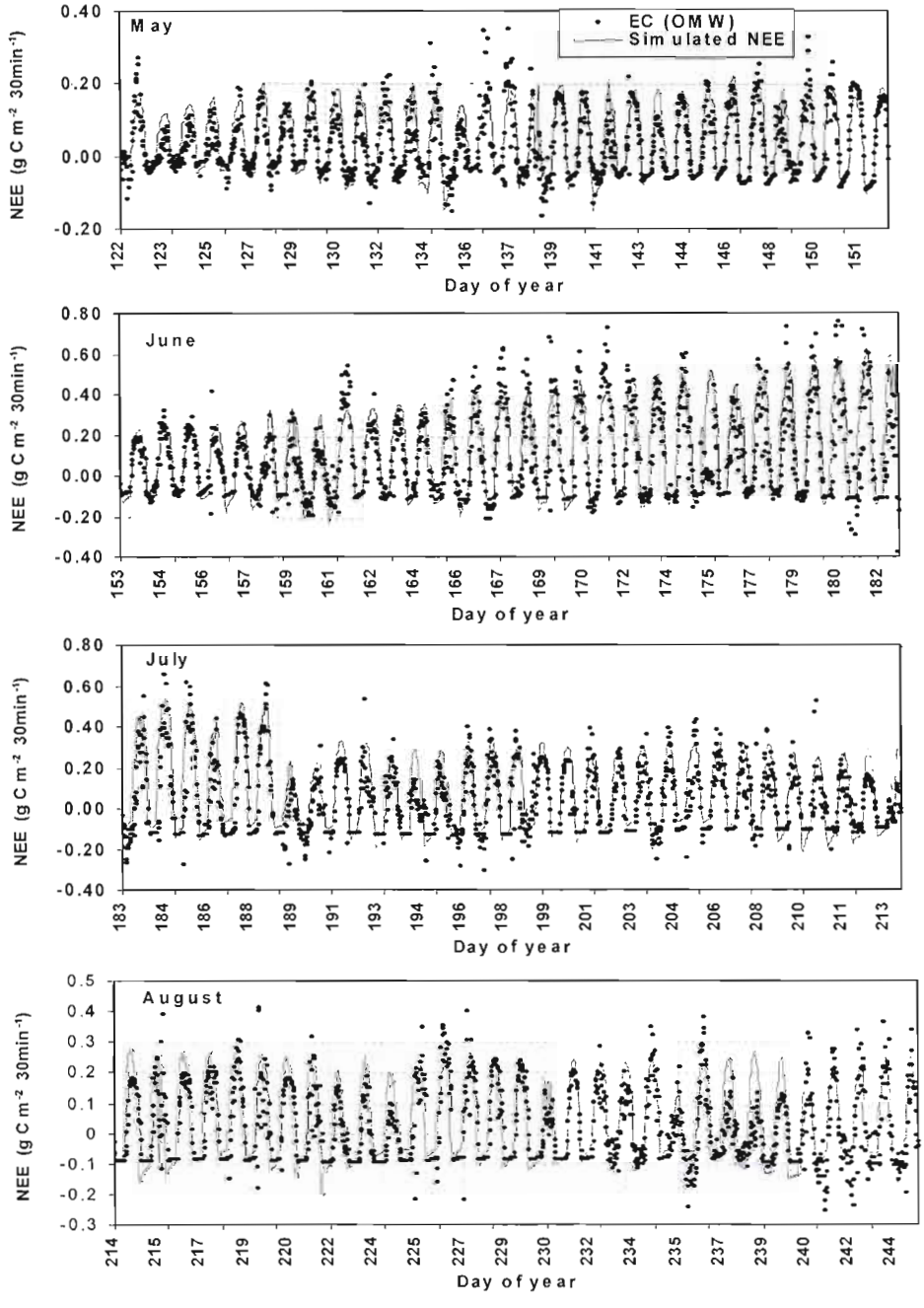

Fig. 3.3. Diurnal dynamics of measured and simulated NEE during the growing season of 2004 in OMW.

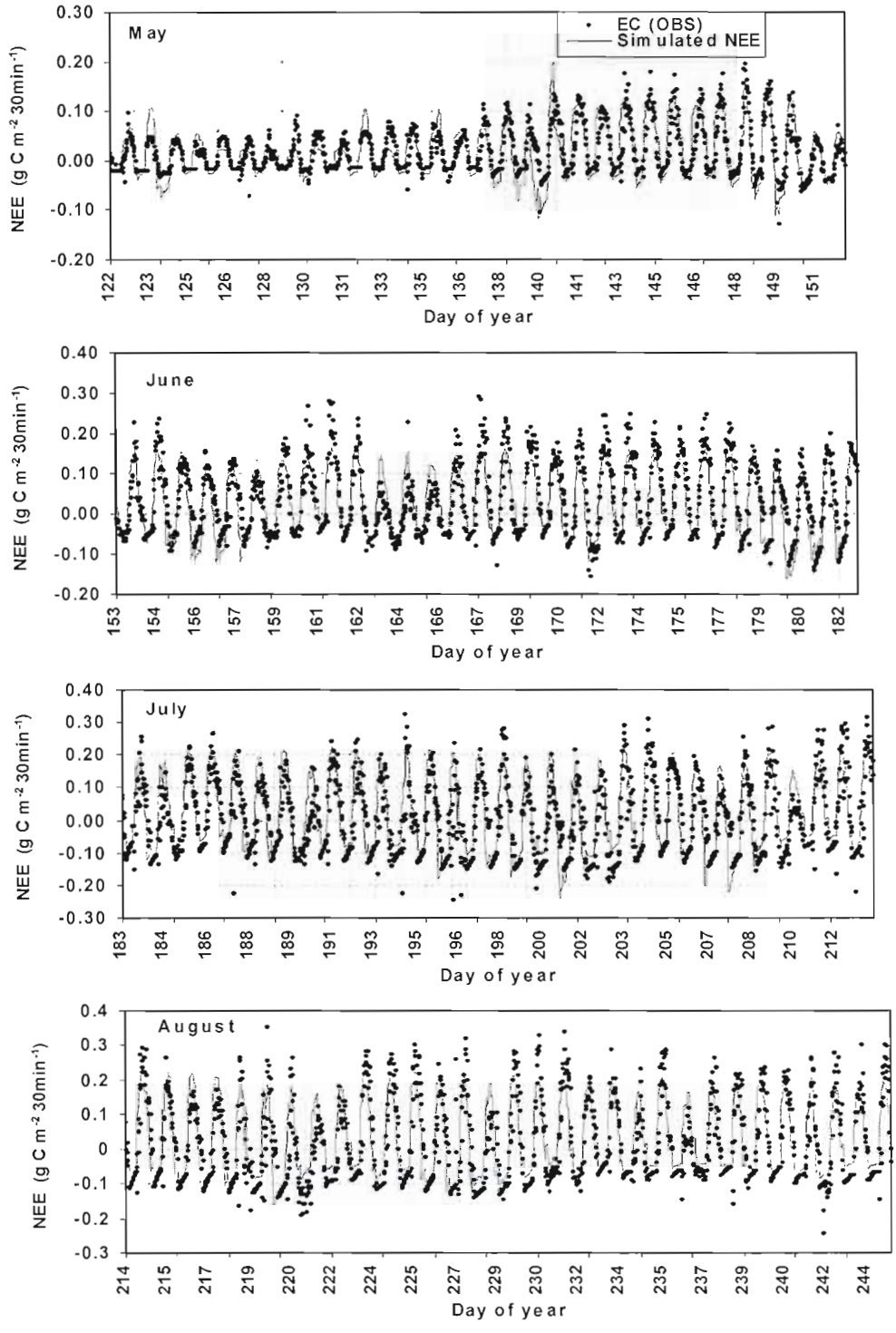

Fig. 3.4. Diurnal dynamics of measured and simulated NEE during the growing season of 2004 in OBS.

For OBS, during the first two weeks of May, the daily and nightly carbon exchange were relatively small, because of low photosynthesic efficiency and respiration. Beginning from the middle of May, the daily photosynthesic efficiency started to increase. By June, the nightly respiratory losses, which are constrained by low soil temperature and air temperature (Grant, 2004), began to increase. From June to August, the daytime peak NEE values were consistently around 0.2 g C m^{-2} $30min^{-1}$. However, the nighttime peak value (around -0.2 g C m^{-2} $30min^{-1}$) only occurred in the middle of July because of the highest temperature during that period.

OMW showed a greater fluctuation in NEE than OBS. The daytime peak of NEE values ranged from 0.2-0.6 g C m^{-2} $30min^{-1}$, while the nighttime peak was less than -0.2 g C m^{-2} $30min^{-1}$. In July, the nighttime respiratory losses were slightly higher than other months. From the end of May, the leaves of deciduous species began to emerge. Daytime NEE gradually increased to a maximum at the middle of June. From the second week of July, the CO_2 flux declined rapidly as a result of the reduction in PPFD. In addition, the variation in cumulative NEE and the ratio of NEE/GEP from May to August for both sites are presented in Fig. 3.5.

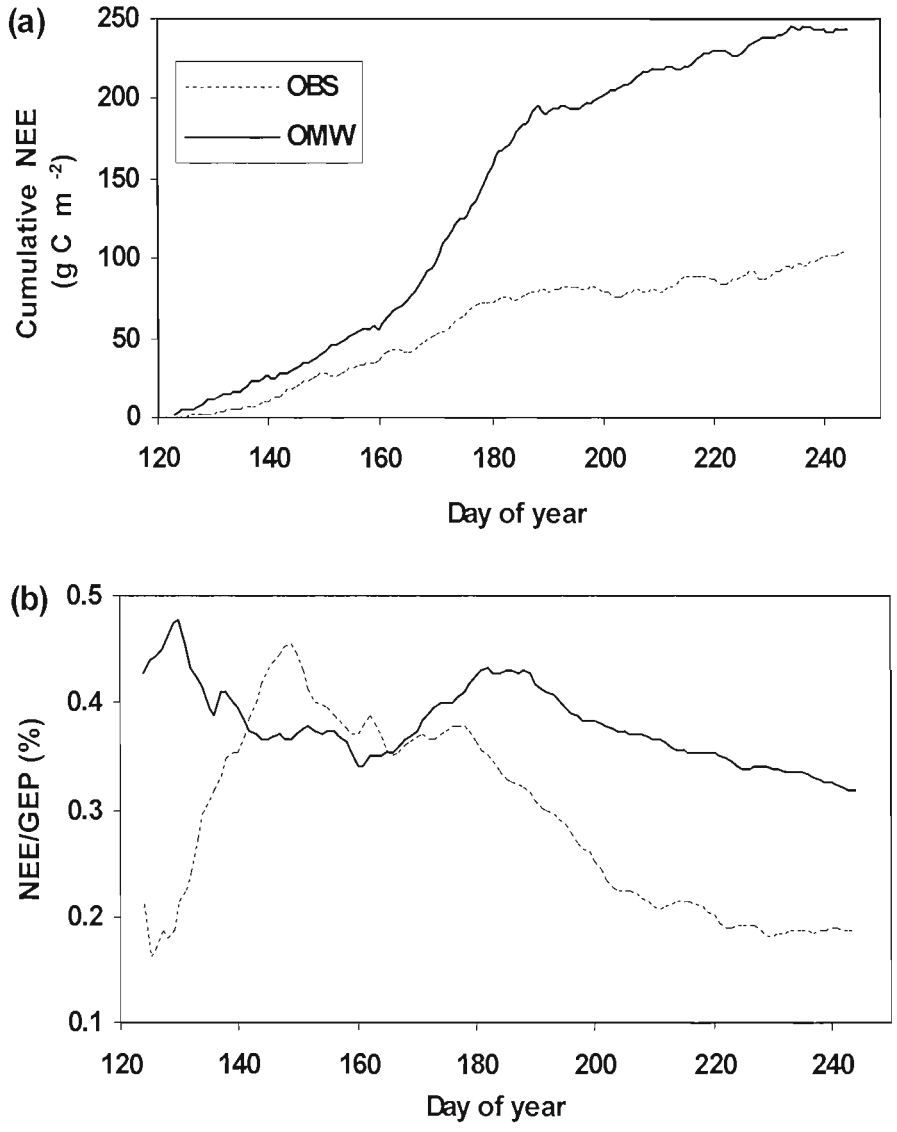

Fig. 3.5. Cumulative net ecosystem exchange of CO_2 (NEE in g C m^{-2}) (a) and ratio of NEE/GEP (b) from May to August of 2004 for both OMW and OBS.

The results demonstrate a notable increase in carbon accumulation for both OMW and OBS throughout the growing season, to a value of about 250 g C m^{-2} for the OMW site and 100 g C m^{-2} for the OBS site at the end of August. Figures 3.6 and 3.7 demonstrate

greater carbon accumulation during the growing season at OMW than at OBS. However, the ratio of NEE/GEP started to decline in July.

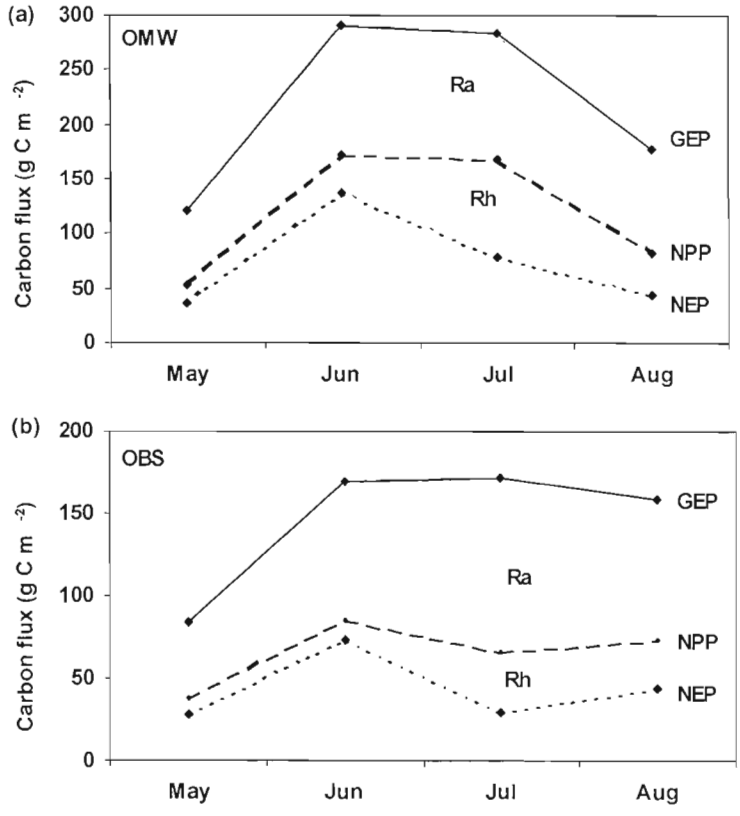

Fig. 3.6. Monthly carbon budgets for the growing season (May – August) of 2004 at (a) OMW and (b) OBS. GEP: gross ecosystem productivity; NPP: net primary productivity; NEE: net ecosystem exchange; Ra: autotrophic respiration; Rh: heterotrophic respiration.

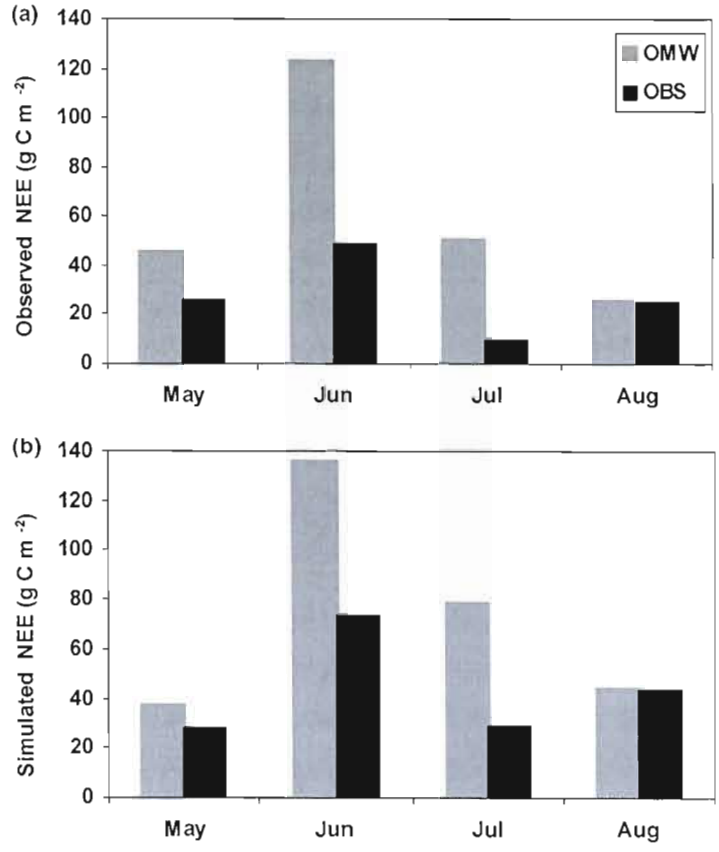

Fig. 3.7. Comparisons of measured and simulated NEE (in g C m^{-2}) for the growing season (May – August) of 2004 in OMW and OBS.

3.5.3 Monthly carbon budgets

The total monthly GEP, NPP and NEP for both sites are presented in Figures 3.6 and 3.7. At OMW, carbon sequestration, including GEP, NPP and NEP, was higher than in OBS, especially in July and August. The carbon use efficiency (CUE, defined as NPP/GEP) at OMW was 0.55, higher than OBS with 0.45. Both values fall within the range of CUE reported by Waring et al. (1998). The maximum monthly NEE was observed in June, because of the maximum PAR and high temperature in this month. On both sites, the July heterotrophic respiration was highest because of the highest air temperature, which is the main reason why the NEE of OBS in July was lower than in

August. This shows that the NEE was controlled by both photosynthesis and respiration, which agrees with the results of Valetini et al (2000). However, due to the infestation of the aspen two-leaf tier moth (Rowlinson, 2004), the NPP of OMW did not reach two times greater than in OBS as reported by Martin et al., (2005).

The results of this study are consistent with previous studies in Saskatchewan and Ontario that reported boreal mixedwood stands have greater productivity and carbon sequestration potential than single-species stands (Kabzems and Senyk, 1967; Opper, 1980; Martin et al., 2005). For example, a recent study of boreal mixedwood forest stands in northern Manitoba, Canada reported by Martin et al (2005) indicated that aboveground biomass carbon was 47% greater in this study than in a pure black spruce stand (Wang et al., 2003) and 44% larger than jack pine stand (Gower et al., 1997). There are several possible mechanisms responsible for higher carbon sequestration rates for mixedwood stands than single species stands: (1) mixedwood stands have a multi-layered canopy with deciduous, shade intolerant aspen over shade tolerant evergreen species that contain a greater foliage mass for a given tree age (Gower et al., 1995); (2) mixedwood forests usually have a lower stocking density (stems per hectare) than those of pure black spruce stands; and (3) mixed-species stands are more resistant and more resilient to natural disturbances. The large amount of boreal mixedwoods and the fact that they represent the most productive segment of boreal landscapes makes them central in forest management. Historically, naturally established mixedwoods were often converted into single-species plantations (Lieffers and Beck, 1994; Lieffers et al., 1996). Mixedwood management is now strongly encouraged by various jurisdictions in Canada (BCMF, 1995; OMNR, 2003).

3.5.4 Relationship between observed NEE and environmental variables

To investigate the influence of air temperature (T) and PPFD on carbon exchanges in both sites, the observations of GEP, ecosystem respiration (ER), and NEE were plotted against measured T (Fig 3.8) and PPFD values (Fig. 3.9). The relationship between mean daily values of GEP, ER, NEE and mean daily temperature (T_d) for growing season is shown in Fig. 3.8. GEP gradually increases with the increase of temperature

(T_d) and becomes stable between 15 - 20°C. This temperature generally coincides with the optimum temperature for maximum NEE occurrence (2 g C m^{-2} day^{-1}). This result is in agreement with the conclusion drawn by Huxman et al (2003) for a subalpine coniferous forest. However, the larger scatter in this relationship was found in OMW, in which the range of GEP was greater than for OBS. Ecosystem respiration was positively correlated with T_d. at both OMW and OBS, and each showed a similar pattern for this relationship (Fig. 3.8).

There is large scatter in the relationship between NEE and mean daily temperature. It seems that NEE is not strongly correlated with T_d in the summer, which is similar to recent reports by Hollinger et al (2004) and FCRN (2004). To compare light use efficiencies and the effects of available radiation on photosynthesis, the relationships between GEP and PPFD during the growing season for both OMW and OBS are shown in Fig. 9. Both GEP and NEE are positively correlated with PPFD for both OMW and OBS. A significant nonlinear relationship (r^2=0.99) between GEP and PPFD was found for both OMW and OBS, which was similar to other studies reported for temperate forest ecosystems (Dolman et al., 2002; Morgenstern et al., 2004; Arain et al., 2005) and boreal forest ecosystems (Law et al., 2002). Also, a very strong nonlinear regression between NEE and PPFD (r^2=0.98) was consistent with the studies of Law et al (2002) and Monson et al (2002).

3.6. CONCLUSION

(1) The TRIPLEX-Flux model performed reasonably well predicting NEE in a mature coniferous forest on the southern edge of the boreal forest in Saskatchewan and a boreal mixedwood in northeastern Ontario. The model is able to capture the diurnal variation in NEE for the growing season (May-August) in both forest stands. Environmental factors such as temperature and photosynthetic photon flux density play an important role in determining both leaf photosynthesis and ecosystem respiration.

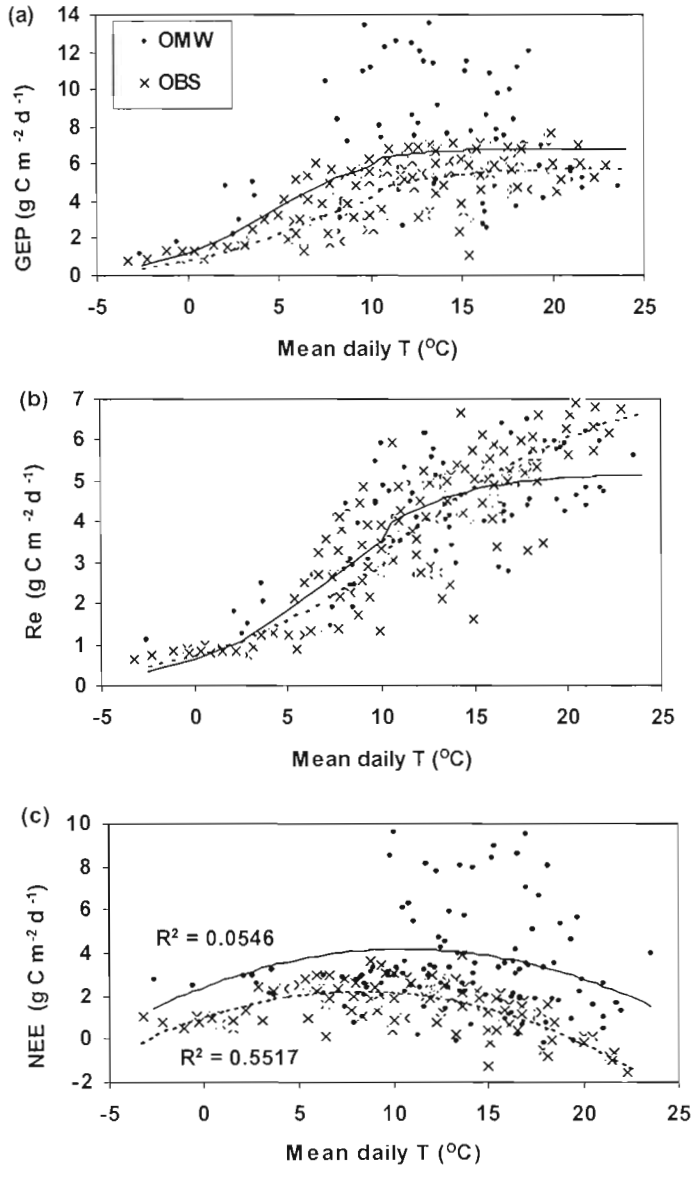

Fig. 3.8. Relationship between the observations of (a) GEP (in g C m^{-2} day^{-1}), (b) ecosystem respiration (in g C m^{-2} day^{-1}), (c) NEE (g C m^{-2} day^{-1}) and mean daily temperature (in °C). The solid and dashed lines refer to the OMW and OBS, respectively.

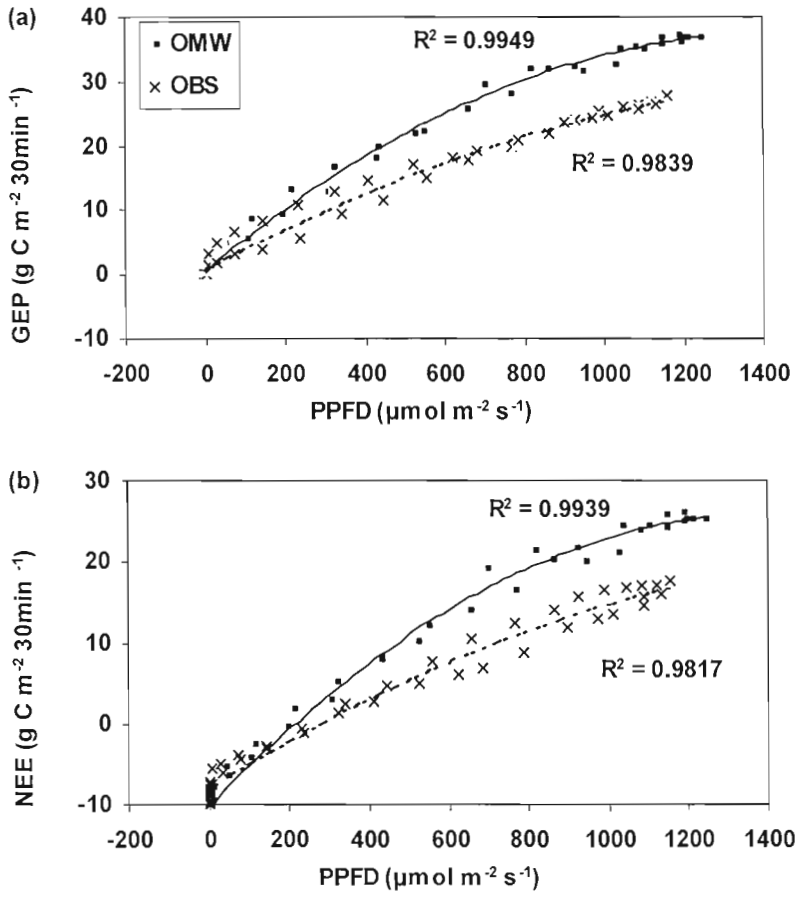

Fig. 3.9. Relationship between the observations of (a) GEP (in g C m^{-2} 30 minutes $^{-1}$), (b) NEE in g C m^{-2} 30 minutes $^{-1}$) and photosynthetic photo flux densities (PPFD) (in μmol m^{-2} s^{-1}). The symbols represent averaged half-hour values.

(2) Compared with the OBS ecosystem, the OMW has several distinguishing features. First, the diurnal pattern was uneven, especially after completed leaf-out of deciduous species in June. Secondly, the response to solar radiation is stronger with superior photosynthetic efficiency and ecosystem gross productivity. Thirdly, carbon use efficiency and the ratio of NEP/GEP are higher. Thus, OMW could potentially uptake more carbon than OBS. Both OMW and OBS were acting as carbon sinks for the atmosphere during the growing season of 2004.

(3) Because of climate change impacts (Singh and Wheaton 1991; Herrington et al., 1997) and ecosystem disturbances, such as fire (Stocks et al., 1998; Flannigan et al., 2001) and insects (Fleming, 2000), the boreal forest distribution and composition could be changed. If the environmental condition becomes warmer and drier, some current single species coniferous ecoregions might be developed into a mixedwood forest type, which would be beneficial to carbon sequestration. Whereas, switching mixedwood forests to pure deciduous forests may lead to reduce carbon storage potential, because the deciduous forests sequester even less carbon than pure coniferous forests (Bond-Lamberty et al., 2005). From the point of view of forest management, the mixedwood forest is suggested as a good option to extend and replace the single species stand, which would enhance the carbon sequestration capacity of Canadian boreal forests, and, therefore, reduce the atmospheric CO_2.

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CHAPTER IV

PARAMETER ESTIMATION AND NET ECOSYSTEM PRODUCTIVITY PREDICTION APPLYING THE MODEL-DATA FUSION APPROACH AT SEVEN FOREST FLUX SITES ACROSS NORTH AMERICA

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4.1. RÉSUMÉ

Les modèles basés sur le processus des écosytèmes terrestres jouent un rôle important dans l'écologie terrestre et dans la gestion des ressources naturelles. Cependant, les hétérogénéités spatio-temporelles inhérentes aux écosystèmes peuvent mener à des incertitudes de prédiction des modèles. Pour réduire les incertitudes de simulation causées par l'imprécision des paramètres des modèles, la méthode de Monte Carlo par chaînes de Markov (MCMC) à été appliquée dans cette étude pour estimer les parametres clé de la sensibilité dans le modèle basé sur le processus de l'écosystème TRIPLEX-Flux. Les quatre paramètres clé sélectionnés comportent : un taux maximum de carboxylation photosynthétique à 25°C (V_{max}), un taux du transport d'un électron (J_{max}) saturé en lumière lors du cycle photosynthétique de réduction du carbone, un coefficient de conductance stomatale (m), et un taux de référence de respiration à 10°C (R_{10}). Les mesures de covariance des flux turbulents du CO_2 échangé ont été assimilées afin d'optimiser les paramètres pour tous les mois de l'année 2006. Sept tours de mesures de flux placées dans des forêts incluant trois forêts à feuilles caduques, trois forêts tempérées à feuillage persistant et une forêt boréale à feuillage persistant, ont été utilisées pour faciliter la compréhension des variations mensuelles des paramètres du modèle. Après que l'optimisation et l'ajustement des paramètres ait été réalisée, la prédiction de la production nette de l'écosystème s'est ameliorée significativement (d'environ 25%) en comparaison aux mesures de flux de CO_2 réalisées sur les sept sites d'écosystème forestier. Les résultats suggèrent, eu égard aux paramètres sélectionnés, qu'une variabilité plus importante se produit dans les forêts à feuilles larges que dans les forêts d'arbres à aiguilles. De plus, les résultats montrent que l'approche par la fusion des données du modèle incorporant la méthode MCMC peut être utilisée pour estimer les paramètres basés sur les mesures de flux et que des paramètres saisonniers optimisés peuvent considérablement améliorer la précision d'un modèle d'écosystème lors de la simulation de sa productivité nette, et cela, pour différents écosystèmes forestiers situés à travers l'Amerique du Nord.

Mots Clefs: Markov Chain Monte Carlo, estimation des paramètres, équilibre du carbone, assimiliation des données, écosystème forestier, modèle TRIPLEX-Flux

4.2. ABSTRACT

Process-based terrestrial ecosystem models play an important role in terrestrial ecology and natural resource management. However, inherent spatial and temporal heterogeneities found within terrestrial ecosystems may lead to prediction uncertainties in models. To reduce simulation uncertainties due to inaccurate model parameters, the Markov Chain Monte Carlo (MCMC) method was applied in this study to estimate sensitive key parameters in a TRIPLEX-Flux process-based ecosystem model. The four key parameters selected include a maximum photosynthetic carboxylation rate of 25°C (V_{max}), an electron transport (J_{max}) light-saturated rate within the photosynthetic carbon reduction cycle of leaves, a coefficient of stomatal conductance (m), and a reference respiration rate of 10°C (R_{10}). Eddy covariance CO_2 exchange measurements were assimilated to optimize the parameters for each month in the year 2006. Seven forest flux tower sites that include three deciduous forests, three evergreen temperate forests, and one evergreen boreal forest were used to facilitate understanding of the monthly variation in model parameters. After parameter optimization and adjustment took place, net ecosystem production prediction significantly improved (by approximately 25%) compared to the CO_2 flux measurements taken at the seven forest ecosystem sites. Results suggest that greater seasonal variability occurs in broadleaf forests in respect to the selected parameters than in needleleaf forests. Moreover, results show that the model-data fusion approach incorporating the MCMC method can be used to estimate parameters based upon flux measurements, and that optimized seasonal parameters can greatly improve ecosystem model accuracy when simulating net ecosystem productivity for different forest ecosystems located across North America.

Keywords: Markov Chain Monte Carlo, parameter estimation, carbon balance, data assimilation, forest ecosystem, TRIPLEX-Flux model

4.3. INTRODUCTION

Process-based terrestrial ecosystem models have been widely applied to investigate the effects of resource management, disturbances, and climate change on ecosystem functions and structures. It has proven to be a big challenge to accurately estimate model parameters and their dynamic range at different spatial-temporal scales due to complex processes and spatial-temporal variabilities found within terrestrial ecosystems. Often, uncertainty in findings is the end result of studies, especially for large-scale estimations. Terrestrial carbon cycle projections derived from multiple coupled ecosystem-climate models, for example, varied in their findings. Discrepancies range from a 10 Gt C/yr sink to a 6 Gt C/yr source by the year 2100 (Kicklighter et al., 1999; Cox et al., 2000; Cramer et al., 2001; Friedlingstein et al., 2001; Friedlingstein et al., 2006). In addition, by comparing nine process-based models applied to a Canadian boreal forest ecosystem, Potter et al., (2001) found that core parameter values and their specific sensitivity to certain key environmental factors were inconsistent due to seasonal and locational variance in factors. Model prediction uncertainties stem primarily from basic model structure, initial conditions, model parameter estimation, data input, natural and anthropogenic disturbance representation, scaling exercises, and the lack of knowledge of ecosystem processes (Clark et al., 2001; Larocque et al., 2008). For time-dependent nonlinear dynamic replications such as a carbon exchange simulation, modelers typically face major challenges when developing appropriate data assimilation tools in which to run models.

Eddy covariance methods that apply micrometeorological towers were adapted to record the continuous exchange of carbon dioxide between terrestrial ecosystems and the atmosphere for the North America Carbon Program (NACP) flux sites. These data sets provide a unique platform in which to understand terrestrial ecosystem carbon cycle processes.

It is increasingly recognized that global carbon cycle research efforts require novel methods and strategies to combine process-based models and data in a systematic manner. This is leading research in the direction of the model-data fusion (MDF)

approach (Raupach et al., 2005; Wang et al., 2009). MDF is a new quantitative approach that provides a high level of empirical constraint on model predictions that are based upon observational data. It typically features both inverse problems and statistical estimations (Tarantola, 2005; Raupach et al, 2005; Evensen, 2007). The key objective of MDF is to improve the performance of models by either optimizing/refining values of unknown parameters and initial state variables or by correcting model predictions (state variables) according to a given data set. The use of MDF for parameter estimation is one of its most common applications (Wang et al, 2007, Fox et al., 2009). Both gradient-based (e.g., Guiot et al., 2000; Wang et al., 2001; Luo et al. 2003; Wu et al., 2009) and non-gradient-based methods (e.g., Mo and Beven, 2004; Braswell et al. 2005; White et al., 2005) have been applied, and their advantages and limitations have been discussed recently in the published literature (Raupach et al., 2005; Wang et al., 2009; Willams et al., 2009). Furthermore, by way of assimilating eddy covariance flux data, several recent studies have been carried out to reduce simulation bias, error, and uncertainties for different forest ecosystems (Braswell et al., 2005; Sacks et al., 2006; Williams et al., 2005; Wang et al., 2007; Mo et al., 2008). Most of these studies were focused on the seasonal variation in estimated parameters and ecosystem productivity. However, in North America, the spatial heterogeneity of key model parameters has been ignored or has not been explicitly considered.

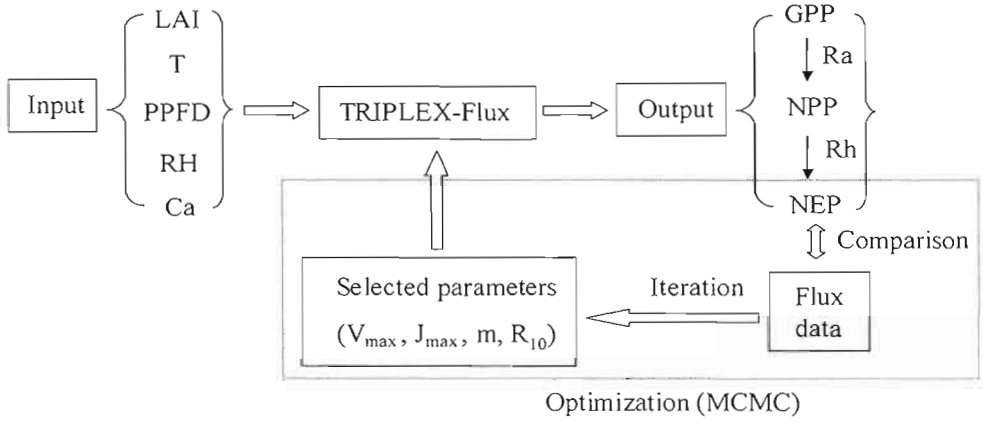

Fig. 4.1. Schematic diagram of the model-data assimilation approach used to estimate parameters. Ra and Rh denote autotrophic and heterotrophic respiration. LAI is the leaf

area index. Ca is the input climate variable CO_2 concentration (ppm) within the atmosphere. T is the air temperature (°C). RH is the relative humidity (%). PPFD is the photosynthetic photon flux density (μmol m^{-2} s^{-1}).

A parameter estimation and data assimilation approach was used in this study to optimize model parameters. Fig. 4.1 provides a schema of the method applied to estimate parameters based upon a process-based ecosystem model and the flux data. The TRIPLEX-Flux model (Zhou et al., 2008; Sun et al., 2008) was recently developed to simulate terrestrial ecosystem productivity, that is, gross primary productivity (GPP), net primary productivity (NPP), net ecosystem productivity (NEP), respiration (autotrophic respiration) (Ra) and heterotrophic respiration (Rh), and the water and energy balance (sensible heat (H) and latent heat (LE) fluxes) by way of half-hourly time steps (Zhou et al, 2008; Sun et al., 2008). The input climate variables include atmospheric CO_2 concentration (Ca), temperature (T), relative humidity (rh), and the photosynthetic photon flux density (PPFD). Half-hourly NEP measurements from CO_2 flux sites were used to estimate TRIPLEX-Flux model parameters. Thus, the major objectives of this study were (1) to test the TRIPLEX-Flux model simulation against flux tower measurements taken at sites that possess different tree species within North America; (2) to estimate certain key parameters sensitive to environmental factors by way of flux data assimilation; and (3) to understand ecosystem productivity spatial heterogeneity by quantifying parameters for different forest ecosystems.

4.4. MATERIALS AND METHODS

4.4.1. Research sites

This study was carried out at seven forest flux sites that were selected from 36 primary sites possessing complete data sets (for 2006) within the NACP Interim Synthesis: Site-Level. Information concerning these seven forest sites is presented in Table 4.1. The study area consists of three evergreen needleleaf temperate forests (ENT), three deciduous broadleaf forests (DB), and one evergreen needleleaf boreal forest (ENB) spread out across Canada and the United States of America. These forest ecosystems are located within different climatic regions with varied annual mean temperatures

(AMT) ranging from 0.4°C to 8.3°C and annual mean precipitation (AMP) ranging from 278mm to 1484mm. The age span of these forest ecosystems ranges from 60 to 111 years and falls within the category of middle and old aged forests, respectively.

Eddy covariance flux data, climate variables (T, rh, and wind speed), and radiation above the canopy were recorded at the flux tower sites. Gap-filled and smoothed LAI data products were accessed from the MODIS website (http://accweb.nascom.nasa.gov/) for each site under the Site-Level Synthesis of the NACP Project (Schwalm et al., 2009), which contains the summary statistics for each eight day period.

Table 4.1. Basic information for all seven study sites

Site Code	State (Country)	Latitude(°N) / Longitude(°W)	Forest type	Age	AMT (°C)	AMP (mm)
CA-Ca1	BC (CA)	49.87 / 125.33	ENT	60	8.3	1461
CA-Oas	SK (CA)	53.63 / 106.20	DB	83	0.4	467
CA-Obs	SK (CA)	53.99 / 105.12	ENB	111	0.4	467
US-Ha1	MA (USA)	42.54 / 72.17	DB	81	8.3	1120
US-Ho1	ME (USA)	45.20 / 68.74	ENT	109	6.7	778
US-Me2	OR (USA)	44.45 / 121.56	ENT	90	6.4	447
US-UMB	MI (USA)	45.56 / 84.71	DB	90	6.2	750

Note: ENB = Evergreen needleleaf boreal forest, ENT = evergreen needleleaf temperate forest, DB = broadleaf deciduous forest.

4.4.2. Model description

The TRIPLEX-Flux model was designed to describe the irradiance and photosynthetic capacity of the canopy as well as to simulate CO_2 flux within forest ecosystems to take advantage of the approach used in a two-leaf mechanistic model (Sun et al., 2008; Zhou et al., 2008). The model itself is composed of two parts: leaf photosynthesis and ecosystem carbon flux. The instantaneous gross photosynthetic rate was derived based upon the biochemical model developed by Farquhar et al. (1980) and the semi-analytical approach developed by Collatz et al. (1991), simulating the photosynthetic effect using the concept of co-limitation developed by Rubisco (V_c) as well as electron transport (V_j). The total canopy photosynthetic rate was simulated using the algorithm developed by De Pury and Farquhar (1997) in which a canopy is divided into sunlit and shaded zones. The model describes the dynamics of abiotic variables such as radiation, irradiation, and diffusion. The net CO_2 assimilation rate (A) was calculated by subtracting leaf dark respiration (Rd) from the above photosynthetic rate:

$$A = \min(Vc,Vj) - R_d \quad (1)$$

This can also be further expressed using stomatal conductance and differences in CO_2 concentrations (Leuning, 1990):

$$A = gs(Ca - Ci)/1.6 \quad (2)$$

Stomatal conductance can be derived in several different ways. For this study, the semi-empirical *gs* model developed by Ball (1988) is used:

$$gs = g0 + 100mArh/Ca \quad (3)$$

NEP is the difference between photosynthetic carbon uptake and respiratory carbon loss, including plant autotrophic respiration (Ra) and heterotrophic respiration (Rh). Rh is dependent on temperature and is calculated using Q_{10} as follows:

$$Rh = R_{10}\, Q_{10}^{(Ts-10)/10} \quad (4)$$

where R_{10} is the reference respiration rate at 10°C; Q_{10} is the temperature sensitivity parameter; and Ts is soil temperature (Lloyd and Taylor, 1994).

4.4.3. Parameters optimization

Although TRIPLEX-Flux considers many parameters, based on sensitivity analysis, the four most sensitive parameters that relate to NEP were selected for this study. In sensitivity analysis, a typical approach (namely, one-at-a-time or OAT) is used to observe the effect of a single parameter change on an output while all other factors are fixed to their central or baseline values. There are three parameters that relate to photosynthesis and the energy balance: V_{max} (the maximum carboxylation rate at 25°C), J_{max} (the light-saturation rate of the electron transport within the photosynthetic carbon reduction cycle of leaves), and m (the coefficient of stomatal conductance). One additional parameter (R_{10}) is used to describe the heterotrophic respiration of ecosystems. Initial values of the three parameters are based upon a previous study. For this version, the parameters have been calibrated for three Fluxnet-Canada Research Network sites: the Groundhog River Flux Station in Ontario and mature black spruce stands found in Saskatchewan and Manitoba (Zhou et al., Sun et al., 2008).

Generally speaking, parameter estimation consists of finding the value of an input parameter vector for which the model output fits a set of observations as much as possible. To optimize model parameters, the simplest and crudest approach is exhaustive sampling. However, it requires a great amount of calculation time to setup since all points on both the temporal or spatial scales must be calibrated. This method, therefore, is not typically recommended for large parameter spaces or modeling scales. An alternative method is the Bayesian approach (Gelman et al., 1995) in which

unidentified parameters may possess the desired probability distribution to describe *a priori* information. Thus, a probability density representing *a posteriori* information of a parameter is inferable from the *a priori* information as well as by means of observations themselves.

The *a priori* information can be defined as $B(x)$ for an input parameter vector x. This information is then combined with information provided by means of a comparison of the model output along with the observational data p=(p_i, i = 1, 2, …, m) in order to define a probability distribution that represents the *a posteriori* information $\beta(x)$ of the parameter vector x:

$$\beta(x) = k \cdot B(x) \cdot L(x)$$

where k is an appropriate normalization constant, and $L(x)$ is the likelihood function that roughly measures the fit between the observed data (p_i, i = 1, 2, . . ., m) and the data predicted $\{p'(x) = [p'_1(x), \ldots, p'_m(x)]\}$ by the model itself. If model errors are assumed to be independent and of Gaussian distribution, $L(x)$ can be written as follows:

$$L(x) = \Pi \left[(2\pi\sigma)^{-0.5} e^{-(u-u')^2 (2\sigma^2)^{-1}}\right]$$

where σ is the error (one standard deviation) for each data point, and u and u' denote the measured and simulated NEP (in g C m^{-2} d^{-1}), respectively. Here, σ represents the data error relative to the given model structure and, thus, represents a combination of measurement error and process representation error.

For the application of Bayes' theorem, an efficient algorithm called the Metropolis–Hastings algorithm (Metropolis et al., 1953; Hastings, 1970) was used to force convergence to occur more quickly towards the best estimates as well as to simulate the probability distribution of the selected parameters. In this study, the Markov chain Monte Carlo (MCMC) method was used to calculate (x) for the given observational vector p. The *a prior* probability density function was first specified by providing a set of limiting intervals for the parameters (m, V_{max}, J_{max}, and R_{10}). The likelihood function was then constructed on the basis of the assumption that errors in the observed data followed Gaussian distributions.

The procedure was designed in four steps based upon the Metropolis-Hastings algorithm as follows: First, a random or arbitrary value was supplied that acted as an initial parameter within its range. Second, a new parameter based upon *a posteriori* probability distribution was generated. Third, the criterion was tested to judge whether the new parameter was acceptable. Fourth, the steps listed above were repeated (Xu et al., 2006). In total, 5000 iterations of probability distribution for each month were carried out before a set of parameters were adjusted and optimized after the test runs were completed.

Table 4.2. Ranges of estimated model parameters.

Symbol	Unit	Range
M (coefficient of stomatal conductance)	Dimensionless	4-14
V_{max} (maximum carboxylation rate at 25°C)	μmol m^{-2} s^{-1}	5-80
J_{max} (light-saturated rate of electron transport)	μmol m^{-2} s^{-1}	10-170
R_{10} (heterotropic respiration rate at 10°C)	μmol m^{-2} s^{-1}	0.1-10

The *a prior* probability density function of the parameters was specified as a uniform distribution with ranges as shown in Table 4.2. Intervals with lower and upper limits were decided upon based on the suggestions offered by Mo et al. (2008) for BOREAS sites in central Canada. Parameter distribution was assumed to be uniform and probability equal for all parameter values that occurred within the intervals. Due to the lack of further knowledge regarding parameter distribution, parameter value limits and their distributions were considered to be *a prior* in regard to the approximate feature of the parameter space.

4.5. RESULTS AND DISCUSSION

4.5.1. Seasonal and spatial parameter variation

Previous studies (Harley et al., 1992; Cai and Dang, 2002; Müller et al., 2005) demonstrated that the stomatal conductance slope (m), which relates to the degree of leaf stomatal opening, was sensitive to atmospheric carbon dioxide levels, leaf nitrogen content, soil temperature, and moisture. This may be the reason that, in this study, the sensitivity of the stomatal conductance parameter varied seasonally and exhibits remarkable differences for different forest systems (Fig. 4.2). Due to leaf development and senescence, parameter change was more obvious in deciduous than evergreen forests. In deciduous forests, this parameter increased rapidly from 1.4 to 11.4 at the beginning of the year when foliage started to arise in May and then decreased slightly afterwards. Between October and December, it decreased rapidly before settling back to 1.4 again. In winter, the stoma opening that occurred within the ENT was obviously higher than in the two other forest systems under study. Results from the black spruce forest sites generally agreed with the corresponding values and ranges that occurred during the growing season (Mo et al., 2008).

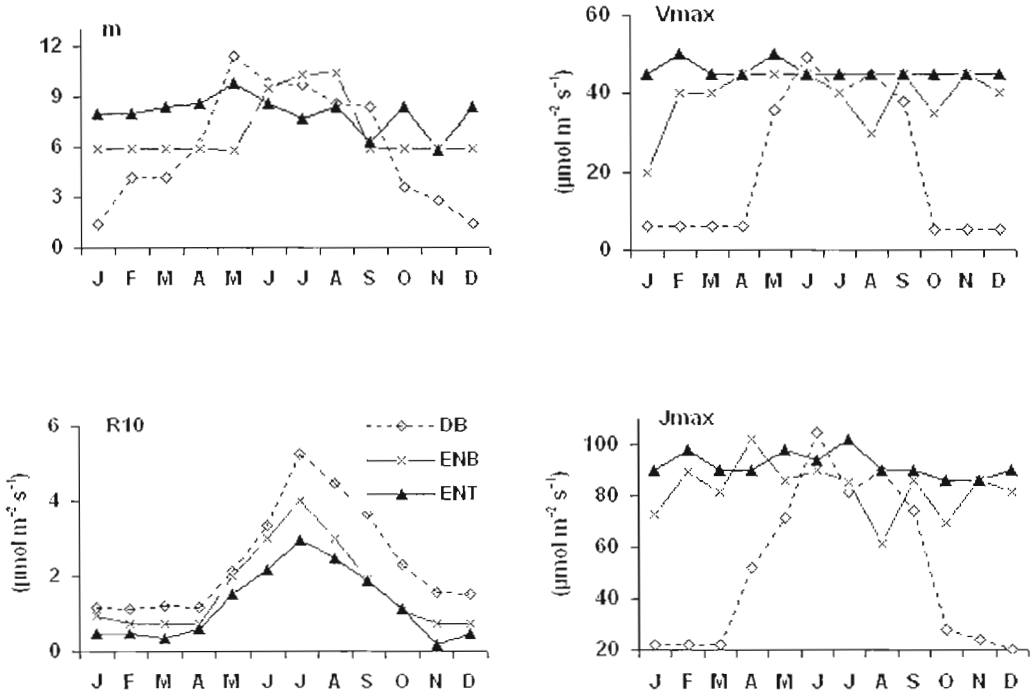

Fig. 4.2. Seasonal variation of parameters for the different forest ecosystems under investigation (2006). DB is the broadleaf deciduous forests that include the CA-OAS, US-Ha1, and US-UMB sites (see Table 1). ENT is the evergreen needleleaf temperate forests that include the CA-Ca1, US-Ho1, and US-Me2 sites. ENB is the evergreen needleleaf boreal forests that include only the CA-Obs site.

As shown in Fig. 4.2, similar seasonal variation patterns were found for both V_{max} and J_{max} in all three selected ecosystem sites. No significant variation was detected in the ENT where only slightly higher values were detected during the summer and only slightly lower values were detected during the winter and fall throughout the period from January to December, 2006. The ENB, on the other hand, returned significantly lower values in the winter, e.g., approximately 20 μmol m^{-2} s^{-1} for V_{max} and 72 μmol m^{-2} $s^{-1}$for J_{max}. In the DB, both V_{max} and J_{max} returned lower values during the winter before rapidly increasing at the start of leaf emergence, reaching their peak values by late June and starting to decline abruptly by the end of August when leaves began to senesce.

Optimization presented a similar trend for the V_{max} and J_{max} parameters that represent the canopy photosynthetic capacity at the reference temperature (25°C) and which are generally assumed to be closely related to leaf Rubisco nitrogen or nitrogen concentrations (Dickinson et al., 2002; Arain et al., 2006). The photosynthetic capacity changed swiftly within deciduous forests during leaf emergence and senescence. This result was consistent with previous studies (Gill et al, 1998; Wang et al, 2007). For evergreen forests, however, no agreement has been reached between previous studies on this subject. While remaining steady and smooth during the entire year in some studies (Dang et al, 1998; Wang et al, 2007), both V_{max} and J_{max} showed strong seasonal trends in other studies (Rayment et al, 2002; Wang et al, 2003; Mo et al, 2008). In this study, no significant seasonal variation was found for V_{max} and J_{max} in both evergreen forest ecosystems (ENT and ENB) for the 2006 reference year.

Results (Fig. 4.2) show that R_{10} was low during the winter then steadily increased throughout the spring, reaching a peak value by the end of July before gradually declining in the fall and returning to the low values observed in the winter. The three selected forest ecosystems used for this study (DB ENB, and ENT) follow identical seasonal variation patterns. The R_{10} value, however, was found to be higher for DB, higher during the middle period for ENT, and lower for ENB. Average R_{10} values during the summer (from June to August) were 4.45, 2.97, and 2.43μmol m^{-2} s^{-1} for DB, ENT, and ENB, respectively.

Due to the inherent complexity of belowground respiration processes and all the other factors mentioned that are in themselves intrinsically interrelated and interactional, various issues remain uncertain. Abundant research has been carried out dealing with this subject by means of applying R_{10} and Q_{10}. Furthermore, both of these factors are spatially heterogeneous and temporal in nature (Yuste et al, 2004; Gaumont-Guay et al, 2006). R_{10} seasonal variation is assumed to be controlled by soil temperature and moisture. In this study, only R_{10} was considered due to its sensitivity to seasonal and spatial variation in temperate and boreal forests (Fig. 4.2).

4.5.2. NEP seasonal and spatial variations

Fig.4.3 shows that the total estimated NEP for each forest site (DB, ENB, and ENT) by the model-data fusion approach was 278.91, 81.55, and 485.39g C m^{-2}, respectively. These numbers are in good agreement with the observational data, although the model simulation seems to have underestimated NEP to a degree. The estimated and observational data demonstrate that all three forest ecosystems under investigation were acting as carbon sinks during the 2006 reference year. The CA-Ca1 (Campbell Douglas-fir) applied in this study is a middle-aged forest that may have greater potential to sequester additional C in the future. Fig.4.4 shows a clear seasonal NEP cycle occurring in the three selected forest ecosystems under investigation. The TRIPLEX-Flux model was able to capture NEP seasonal variation for all three diverse forest ecosystems located across North America.

NEP is typically underestimated during winter and overestimated during summer before parameter optimization (data assimilation) occurs. Taking the entire simulated period into account, MCMC-based model simulations (the right panels in Fig. 4.5) can interpret 72%, 74%, and 84% of NEP measurement variance for ENT, ENB, and DB, respectively. These results are a significant improvement in simulation accuracy compared to the before parameter estimation results (the left panels in Fig. 4.5) that only interprets 42%, 40%, and 63%, respectively, for the three forest ecosystems under investigation.

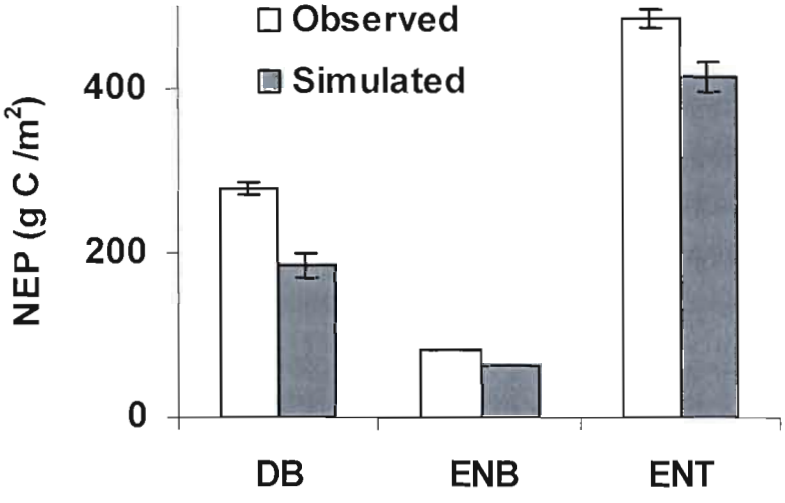

Fig. 4.3. Comparison between observed and simulated total NEP for the different forest types (2006).

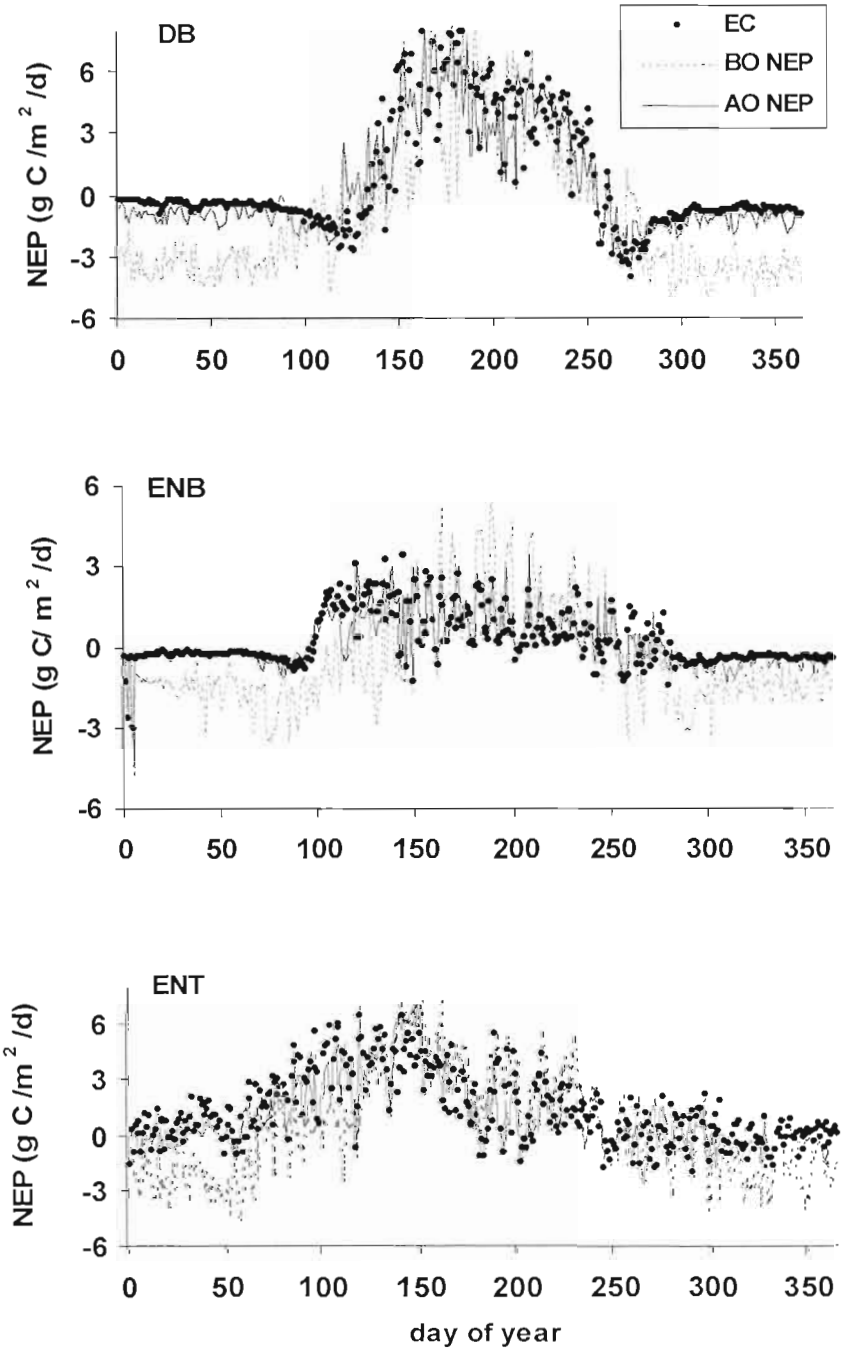

Fig. 4.4. NEP seasonal variation for the different forest ecosystems under investigation (2006). EC is eddy covariance; BO is before model parameter optimization; and AO is after model parameter optimization.

4.5.3. Inter-annual comparison of observed and modeled NEP

Fig. 4.6 compares daily NEP flux results simulated by the optimized and constant parameters in the selected BERMS-Old Aspen site (Table 4.2). However, only 2006 NEP observational data were used for the model simulations during the data assimilation process. The 2004 and 2005 NEP observational data were applied solely for model testing. Optimized flux was very close to the observational data as indicated along the 1:1 line (Fig. 4.7b) whereas flux estimated using constant parameters possessed systematic errors when compared to the 1:1 line (Fig. 4.7a). All linear regression equations involving assimilated and observed NEP indicated no significant bias (P value< 0.05). The simulation that applied constant parameters generated larger bias. The model-data fusion approach accounted for approximately 79% of variation in the NEP observational data whereas the standard model lacking optimization only explained 54% of NEP variation. After parameter optimization, NEP prediction accuracy improved by approximately 25% compared to the CO_2 flux measurements applied to this study.

4.5.4. Impacts of iteration and implications and improvement for the model-data fusion approach

Iteration numbers were analyzed in order to take into account efficiency effects on data assimilation. Further model experimental runs showed that convergence of the Monte Carlo sampling chains appeared after 5000 successive iteration events. No significant difference was observed between 5,000 and 10,000 iteration events (i.e., approximately 4% variation for the simulated monthly NEP). This may be associated with the relatively simple structure of the model and that only four parameters in total were used in this study. However, there is no guarantee that convergence toward an optimal solution using the MCMC algorithm will occur when complexity is added to a simulation model by way of an increase in parameter numbers (Wu et al., 2009).

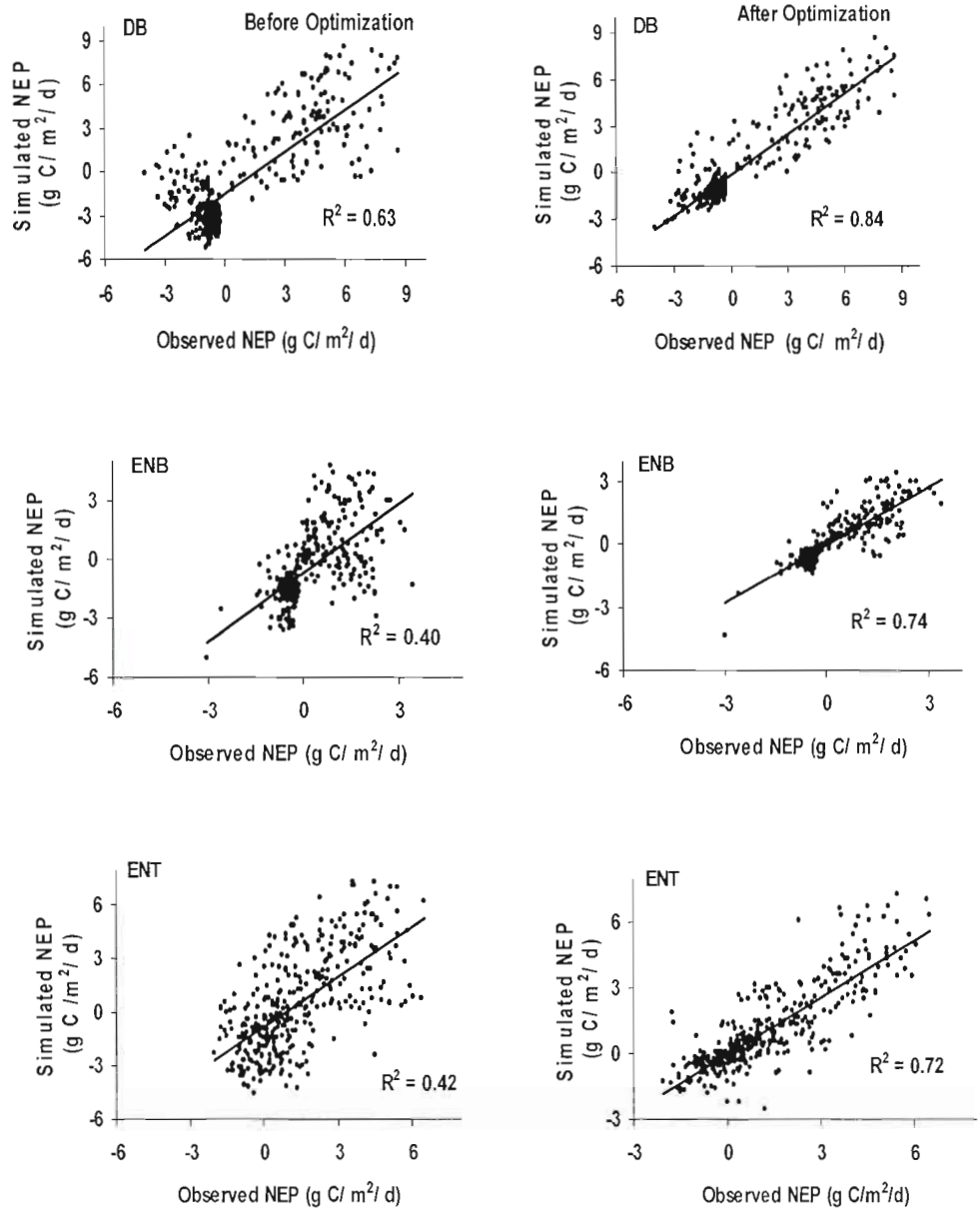

Fig. 4.5. Comparison between observed and simulated daily NEP in which the before parameter optimization is displayed in the left panel and the after parameter optimization is displayed in the right panel. ENT, DB, and ENB denote evergreen needleleaf temperate forests, three broadleaf deciduous forests, and an evergreen needleleaf boreal forest, respectively. A total of 365 plots were setup at each site in 2006.

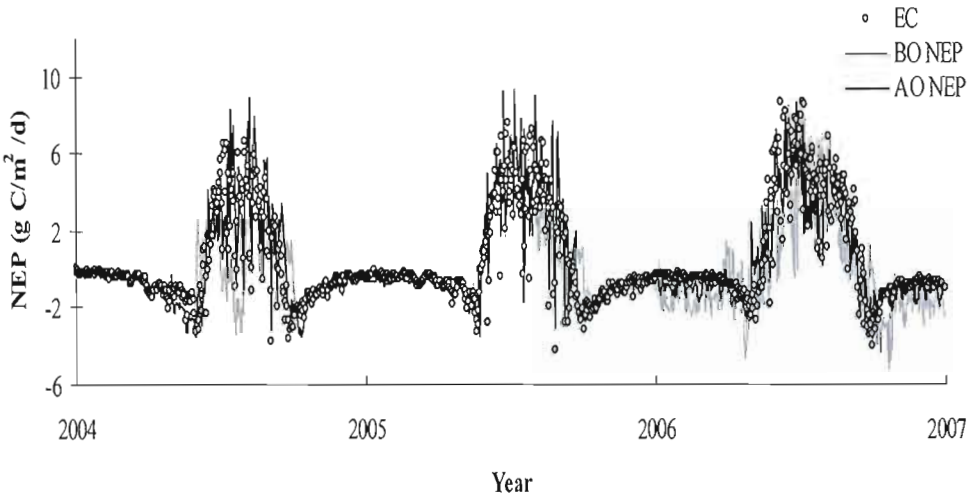

Fig. 4.6. Inter-annual variation of predicted daily NEP flux and observational data for the selected BERMS- Old Aspen (CA-Oas) site from 2004 to 2007. Only 2006 observational data was used to optimize model parameters and simulated NEP. Observational data from the other years was used solely as test periods. EC is eddy covariance; BO is before optimization; and AO is after optimization.

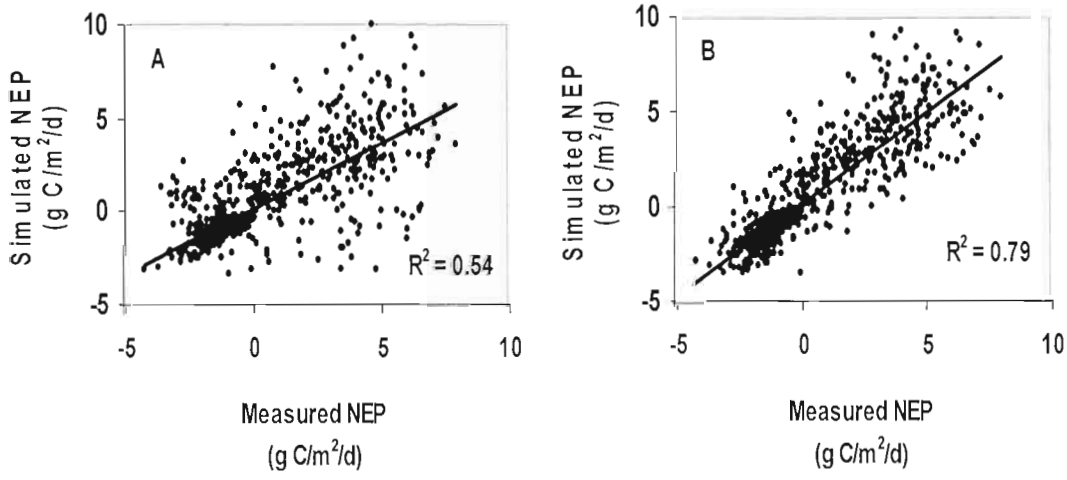

Fig. 4.7. Comparison between observed and simulated NEP. A is before optimization and B is after optimization.

The application of the MCMC approach to estimate key model parameters using NEP flux observational data provides insight into both the data and the models themselves. In the case of certain parameters in which no direct measurement technique is available, values consistent with flux measurements can be estimated. For example, Wang et al. (2001) showed that three to five parameters in a process-based ecosystem model could be independently estimated by using eddy covariance flux measurements of NEP, sensible heat, and water vapor. Braswell et al. (2005) estimated Harvard Forest carbon cycle parameters with the Metropolis-Hastings algorithm and found that most parameters are highly constrained, and the estimated parameters can simultaneously fit both diurnal and seasonal variability patterns. Sacks et al. (2006) also found that soil microbial metabolic processes were quite different in summer and winter based upon parameter optimization used within the simplified PnET model. The parameter estimation studies mentioned above, however, if assuming the application of time-invariant parameters, are based upon eddy covariance flux batch calibration rather than sequential data assimilation. To account for the seasonal variation of parameters, Mo et al. (2008) recently used sequential data assimilation with an ensemble Kalman filter to optimize key parameters of the Boreal Ecosystem Productivity Simulator (BEPS) model, taking into account input errors, parameters, and observational data. Their results suggest that parameters vary significantly for seasonal and inter-annual scales, which is consistent with findings in the present study.

Results here also suggest that the photosynthetic capacity (V_{max} and J_{max}) typically increases rapidly at the leaf expansion stage and reaches a peak in the early summer before an abrupt decrease occurs when foliage senescence takes place in the fall. The results also imply the necessity of model structure improvement. Parameterization for certain processes in the TRIPLEX-flux model is still incomplete due to significant seasonal and inter-annual variations for the photosynthetic and respiration parameters. These parameters (such as m, V_{max}, and J_{max}) were evaluated as steady (or constant) values before parameter adjustment, which may cause notable model prediction deviation and uncertainties to occur under unexpected climate conditions such as drought (Mo et al., 2006, Wilson et al., 2001). The data assimilation approach,

however, is not a panacea. It is, rather, a model-based approach that is highly dependent upon the quality of the carbon ecosystem model itself. Model improvements must be continued such as including impacts of ecosystem disturbances (e.g., fire and logging) on certain key processes (photosynthetic and respiration) as well as including carbon-nitrogen interactions and feedbacks that are currently absent from the TRIPLEX-flux model used in this study. This should certainly be investigated in future studies.

4.6. CONCLUSION

To reduce simulation uncertainties from spatial and seasonal heterogeneity, this study presented an optimization of model parameters to estimate four key parameters (m, V_{max}, J_{max}, and R_{10}) using the process-based TRIPLEX-Flux model. The MCMC simulation was carried out based upon the Metropolis-Hastings algorithm. After parameter optimization, the prediction of net ecosystem production was improved by approximately 25% compared to CO_2 flux measurements measured for this study. The bigger seasonal variability of these parameters was observed in broadleaf deciduous forests rather than needleleaf forests, implying that the estimated parameters are more sensitive to future climate change in deciduous forests than in coniferous forests. This study also demonstrates that parameter estimation by carbon flux data assimilation can significantly improve NEP prediction results and reduce model simulation errors.

4.7. ACKNOWLEDGEMENTS

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CHAPTER V

CARBON DYNAMICS, MATURITY AGE, AND STAND DENSITY MANAGEMENT DIAGRAM OF BLACK SPRUCE FORESTS STANDS LOCATED IN EASTERN CANADA: A CASE STUDY USING THE TRIPLEX MODEL

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5.1. RÉSUMÉ

Comprendre les relations qui existent entre la densité d'un peuplement forestier et sa capacité de stockage du carbone, cela à des étapes variées de son développement, est nécessaire pour gérer la composante de la forêt qui fait partie du cycle global du carbone. Pour cette étude, le volume d'un peuplement et la quantité de carbone de la biomasse aérienne des forêts québecoises d'épinette noire sont simulés en relation avec l'âge du peuplement au moyen du modèle TRIPLEX. Ce modèle a été validé en utilisant à la fois une tour de mesure de flux et des données d'un inventaire forestier. Les simulations se sont avérées réussies. Les corrélations entre les données observées et les données simulées (R^2) étaient de 0.94, 0.93 et 0.71 respectivement pour le diamètre à hauteur de poitrine (DBH), la moyenne de la hauteur du peuplement et la productivité nette de l'écosystème. En se basant sur les résultats de la simulation, il est possible de déterminer l'âge de maturité du carbone du peuplement consideré comme se produisant à l'époque où le peulement de la forêt prélève le maximum de carbone, avant que la récolte finale ne soit realisée. Après avoir comparé l'âge de maturité selon le volume des peuplements considérés (d'environ 65 ans) et l'âge de maturité du carbone des peuplements considérés (d'environ 85 ans), les résultats suggèrent que la récolte d'un même peuplement à son âge de maturité selon le volume est prématuré. Décaler la récolte d'environ vingt ans et permettre au peuplement considéré d'atteindre l'âge auquel sa maturité selon le carbone survient pourrait mener à la formation d'un puits potentiellement important de carbone. Un diagramme de la gestion de la densité du carbone du peuplement considéré, a été développé pour démontrer quantitativement les relations entre les densités de peuplement, le volume du peuplement et la quantité de carbone de la biomasse au-dessus du sol, cela à des stades de développement variés, dans le but de déterminer des régimes de gestion de la densité optimale pour le rendement en volume et le stockage du carbone.

Mots clefs: maturité de la forêt, épinette noire, modèle TRIPLEX

5.2 ABSTRACT

Understanding relationships that exist between forest stand density and its carbon storage capacity at various stand developmental stages is necessary to manage the forest component that is part of the interconnected global carbon cycle. For this study, stand volume and the aboveground biomass carbon quantity of black spruce (*Picea mariana*) forests in Québec are simulated in relation to stand age by means of the TRIPLEX model. The model was validated using both a flux tower and forest inventory data. Simulations proved successful. The correlation between observational data and simulated data (R^2) is 0.94, 0.93, and 0.71 for diameter at breast height (DBH), mean stand height, and net ecosystem productivity (NEP), respectively. Based on simulation results, it is possible to determine the age of a forest stand at which carbon maturity occurs as it is believed to take place at the time when a stand uptakes the maximum amount of carbon before final harvesting occurs. After comparing stand volume maturity age (approximately 65 years old) and stand carbon maturity age (approximately 85 years old), results suggest that harvesting a stand at its volume maturity age is premature. Postponing harvesting by approximately 20 years and allowing the stand to reach the age at which carbon maturity takes place may lead to the formation of a potentially large carbon sink. A novel carbon stand density management diagram (CSDMD) has been developed to quantitatively demonstrate relationships between stand densities and stand volume and aboveground biomass carbon quantity at various stand developmental stages in order to determine optimal density management regimes for volume yield and carbon storage.

Key words: forest maturity, SDMD, black spruce, TRIPLEX model

5.3 INTRODUCTION

Forest ecosystems play a key role in the interconnected global carbon cycle due to their potential capacity as terrestrial carbon storage reservoirs (in terms of living biomass, forest soils, and products). They act as both a sink and a source of atmospheric carbon dioxide, removing CO_2 from the atmosphere by way of carbon sequestration via photosynthesis as well as releasing CO_2 by way of respiration and forest fires. Among these ecological and physiological processes, carbon exchange between forest ecosystems and the atmosphere are influenced not only by environmental variables (e.g., climate and soil) but also by anthropogenic activities (e.g., clear cutting, planting, thinning, fire suppression, insect and disease control, fertilization, etc.). In recent years, increasing attention has been given to the capacity of carbon mitigation under improved forest management initiatives due to the prevalent issue of climate change. Reports issued by the Intergovernmental Panel on Climate Change (*IPCC*) (IPCC 1995, 1996) recommend that the application of a variety of improved forest managerial strategies (such as thinning, extending periods between rotation treatments, etc.) could enhance the capacity of carbon conservation and mitigate carbon emissions in forested lands, thus helping to restrain the increasing rate of CO_2 concentrations within the atmosphere. To move from concept to practical application of forest carbon management, there remains an urgent need to better understand how management activities regulate the cycling and sequestration of carbon.

Rotation age is the length of the overall harvest cycle. A forest should have reached maturity stage by this age and be ready to be harvested for sustainable yield practices. In forest management, the culmination point of the mean annual increment (MAI) is an important criterion to determine rotation age. For example, the National Forest Management Act (NFMA) of 1976 (Public Law 94-588) issued by the United States of America specifies that the national forest system must generally have reached the culmination point of MAI before harvesting can be permitted. However, an earlier study has suggested that this conventional stand maturity harvesting age statute may reduce the mean carbon storage capacity of trees to one-third of their maximum

amount if followed accordingly (Cooper, 1983). Using a case study of a beech forest located in Spain as an example, Romero et al. (1998) determined the optimal harvesting rotation age, taking into account both timber production and carbon uptake. Moreover, in Finland, Liski et al. (2004) also suggested that a longer Scots pine and Norway spruce stand rotation length would favor overall carbon sequestration. Lastly, Alexandrov (2007) showed that the age dependence of forest biomass is a power-law monomial, suggesting that the annual magnitude of a carbon sink induced by delayed harvesting could increase the baseline carbon stock by 1% to 2%.

Crown closure and an increase in competition may cause forest health problems and a decline in growth during stand development. Stand density, therefore, must be adjusted by means of thinning. After thinning, stems are typically removed from stands. This has an effect on total tree number, the leaf area index (LAI), and transient biomass reduction (Davi et al., 2008). Thinning is regarded as a strategy to improve stand structure, habitat quality, and carbon storage capacity (Alam et al., 2008; Horner et al., 2010).

A stand density management diagram (SDMD) is a stand-level model used to determine thinning intensity based on the relationship between yield and density at different stages of stand development (Newton, 1997). SDMD has received considerable attention with regards to timber yield (Newton, 2003, Stankova and Shibuya, 2007, Castedo-Dorado et al., 2009), but its carbon storage benefits have largely been ignored. No relationship between carbon sequestration, tree volume, stand density, and maturity age has been documented up to now. To the knowledge of the authors, this study is the first attempt to quantify these relationships and develop a management-oriented carbon stand density management diagram (CSDMD) at the stand level for black spruce forests in Canada. Newton (2006) attempted to determine optimal density management in regard to net production within black spruce forests. However, since his SDMD model was developed at the individual tree level, it is difficult to scale up the model to a stand or landscape level by using diameter distribution (Newton et al., 2004; Newton et al., 2005).

Within the eastern Canadian boreal forest, black spruce remains a popular species that is extremely important natural resource for both local economies and the country at large, supplying timber to large industries in the form of construction material and paper products. Black spruce matures between 50 and 120 years with an average stand rotation age of 70 to 80 years (Bell, 1991). Harvesting impacts on carbon cycling are still not clearly understood due to the complex interactions that take place between stand properties, site conditions, climate, and management operations.

In recent years, process-based simulation models that integrate physiological growth mechanisms have demonstrated competence in their ability to quantitatively verify the effects of various silvicultural techniques on forest carbon sequestration. For example, the effects of harvesting regimes and silvicultural practices on carbon dynamics and sequestration were estimated for different forest ecosystems using CENTURY 4.0 (Peng et al., 2002) in combination with STANDCARB (Harmon and Marks, 2002). However, due to the lack of carbon allocation processes, these models were not able to provide quantitative information concerning the relationship between stand age, density, and carbon stocks. A hybrid TRIPLEX model (Peng et al., 2002) was used in this study to examine the impacts of stand age and density on carbon stocks by means of simulating forest growth and carbon dynamics over forest development. TRIPLEX was designed as a hybrid that includes both empirical and mechanistic components to capture key processes and important interactions between carbon and nitrogen cycles that occur in forest ecosystems. Fig. 5.1 provides a schematic of the primary steps in the development of a SDMD based upon simulations produced by TRIPLEX.

The overall objective of this study was to quantitatively clarify the effects of thinning and rotation age on carbon dynamics and storage within a boreal black spruce forest ecosystem and to develop a novel management-oriented carbon stand density management diagram (CSDMD). TRIPLEX was specifically used to address the following three questions: (1) does the optimal rotation age differ between volume yield and carbon storage (2) if different, how much more or less time is required to

reach maximum carbon sequestration? Finally, (3) what is the relationship between stand density and carbon storage in regard to various forest developmental stages? If all three questions can be answered with confidence then maximum carbon storage capacity should be able to be attained by thinning and harvesting in a rational and sustainable manner.

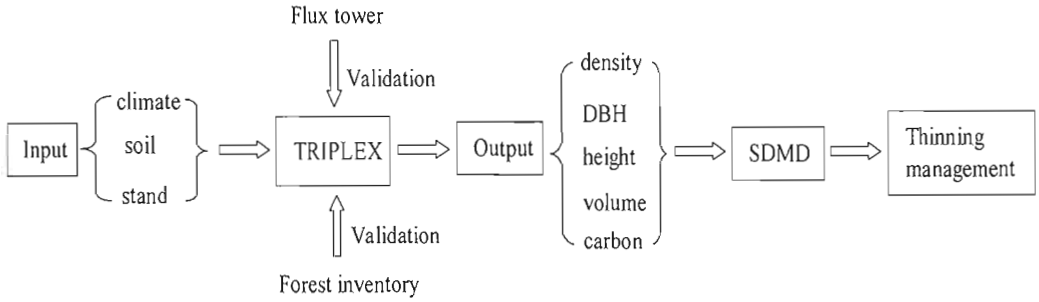

Fig. 5.1. Schematic diagram of the development of the stand density management diagram (SDMD). Climate, soil, and stand information are the key inputs that run the TRIPLEX model. Flux tower and forest inventory data were used to validate the model. Finally, the SDMD was constructed based on model simulation results (e.g., density, DBH, height, volume, and carbon).

5.4. METHODS

5.4.1 Study area

The study area incorporates 279 boreal forest stands (polygons) for a total area of 6275ha. It is located 50km south of Chibougamau (Québec) (Fig. 5.2). Black spruce is the dominant species in 201 of the forest stands within the study area that also include lesser numbers of jack pine, balsam fir, larch, trembling aspen, and white birch. Since 2003, an eddy covariance flux tower (lat 49.69°N and long 74.34°W) has been put into service by the Canadian Carbon Program-Fluxnet Canada Research Network (CCP-FCRN) in one of the stands to continuously measure CO_2 flux at a half-hour time step. This tower also has the ability to collect a large database of ancillary environmental

measurements that can be processed into parameter values used for process-based models and model output verification.

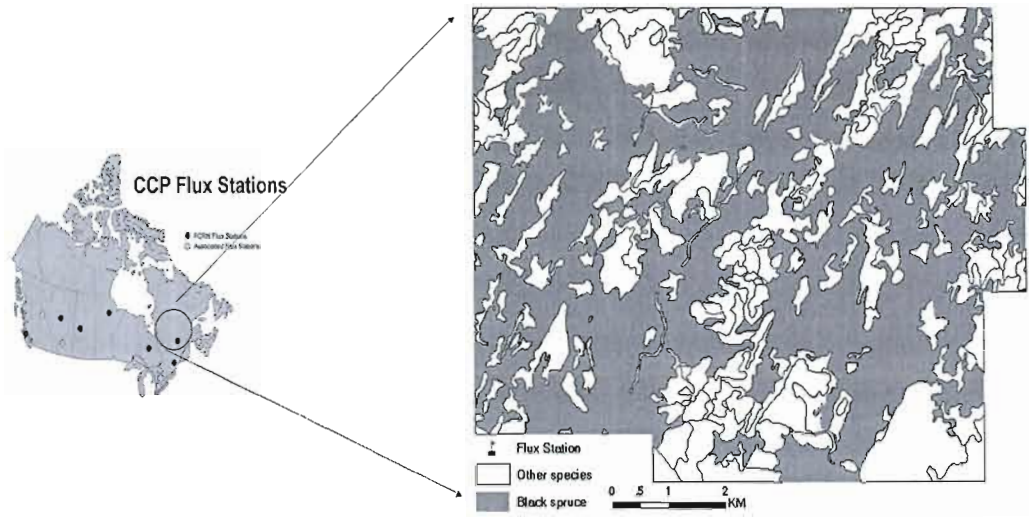

Fig. 5.2. Black spruce (*Picea mariana*) forest distribution study area located within Chibougamau, Québec, Canada.

Mean annual temperature and precipitation in the region is -0.38°C and 959.83mm, respectively. The forest floor is typically covered by moss, sphagnum, and lichen. Additional detailed information concerning site conditions and flux measurements can be found in Bergeron et al, 2008.

5.4.2. TRIPLEX model description

TRIPLEX 1.0 (Peng et al., 2002) can predict forest growth and yield at a stand level applying a monthly time step. By inputting the monthly mean temperature, precipitation, and relative humidity for a given forest ecosystem, the model can simulate key processes for both carbon and nitrogen cycles. TRIPLEX 1.5, an improved version of TRIPLEX that has recently been developed, contains six major modules that carry out specific functions. These modules are explained below:

1. Photosynthetically active radiation (PAR) submodel: PAR was calculated as a function of the solar constant, radiation fraction, solar height, and atmospheric absorption. Forest production and C and N dynamics are primarily driven by solar radiation.

2. Gross primary production (GPP) submodel: GPP was estimated as a function of monthly mean air temperature, forest age, soil drought, nitrogen limitation, and the percentage of frost days during a one month interlude as well as the leaf area index (LAI).

3. Net primary productivity (NPP) submodel: NPP was initially calculated as a constant ratio to GPP (approximately 0.47 for boreal forests) (Peng et al., 2002; Zhou et al., 2005) and was then estimated as the difference between GPP and autotrophic respiration (Ra) (Zhou et al., 2008; Sun et al., 2008; Peng et al., 2009).

4. Forest growth and yield submodel: NPP is proportionally allocated to stems, branches, foliage, and roots. The key variables used in this submodel (tree diameter and height increments) were calculated using a function of the stem wood biomass increment developed by Bossel (1996).

5. Soil carbon and nitrogen submodel: This submodel is based on soil decomposition modules found within the CENTURY model (Parton et al., 1993) while soil carbon decomposition rates for each carbon pool were calculated as the function of maximum decomposition rates, soil moisture, and soil temperature.

6. Soil water submodel: This submodel is based on the CENTURY model (Parton et al., 1993). It calculates monthly water loss through transpiration and evaporation, soil water content, and snow water content (meltwater).

A more detailed description of the improved TRIPLEX 1.5 model can be found in Zhou et al., 2005.

5.4.3. Data sources

5.4.3.1 Model input data

Forest stand as well as climate and soil texture data were required as inputs to use to simulate carbon dynamics and forest growth conditions of the ecosystem under study. Moreover, stand data related to tree age, stocking level, site class, and tree species was further required to simulate each stand separately. Stand data were derived from the 1998 forest cover map as well as aerial photograph interpretation. Photographs interpreted data were calibrated using ground sample plot data (Bernier et al., 2010). Forest growth, productivity, biomass, and soil carbon monthly climatic variables were input into the simulations. Half-hourly weather data from 2003 onwards were obtained by means of the Chibougamau mature black spruce flux tower QC-OBS, a Canadian Carbon Program-Fluxnet Canada Research Network (CCP-FCRN) station located within the study area, and used to compile daily meteorological records throughout this extended period. Daily records and soil texture data prior to this date were provided by Historical Carbon Model Intercomparison Project initiated by CCP-FCRN (Bernier et al., 2010).

5.4.3.2 Model validation data

(1) Forest stand data

To validate forest growth, three circular plots 0.025ha in dimension were established in June, 2009, to first estimate forest dynamics and then validate the TRIPLEX model independently (Table 5.1).

Table 5.1. 2009 stand variables of the three black spruce stands under investigation for TRIPLEX model validation

	Stand 1	Stand 2	Stand 3	Mean
Density (stems/ha)	1735	1800	1915	1817
Mean DBH (cm)	13.98	13.33	11.98	13.10
Mean stand Height (m)	15.89	14.23	13.65	14.59
Mean Volume (m^3/ha)	173.42	146.48	120.74	146.88

All three stands were even-aged black spruce/moss boreal forest ecosystems that had burned approximately 100 years ago. DBH was measured for every stem located within each plot. Moreover, the height of three individual black spruce trees was measured by means of a clinometer in each individual plot, and an increment borer was also used to extract tree ring data at breast height. DBH growth was then estimated using collected radial increment cores. Since it is considered one of the best nonlinear functions available to describe H-DBH relationships for black spruce (Pienaar and Turnbull, 1973; Peng et al., 2004), the Chapman-Richards growth function was chosen to estimate height increments based on DBH growth. This growth function can be expressed as:

$$H = 1.3 + a\,(1 - e^{-b*DBH})^{c} \quad (1)$$

where a, b, and c are the asymptote, scale, and shape parameters, respectively. SPSS 11.0 software for Windows (SPSS, Inc.) was used to estimate model parameters and associated regression statistical information. Using height and DBH field measurements, parameters of the three models (e.g., a, b, and c) and statistical information related to the growth function were estimated as follows: a = 23.93, b = 0.07, and c = 1.71, respectively; the coefficient of determination (r^2) = 0.81.

(2) Flux tower data

TRPLEX 1.5 calculated average tree height and diameter increments from the increments within the stem woody mass. With such a structure, the model produced reasonable output data related to growth and yield that reflects the impact of climate variability over a period of time. To test model accuracy (with the exception of forest growth), simulated net ecosystem productivity (NEP) was compared to the eddy covariance (EC) flux tower data. Half-hourly weather flux data gathered from 2003 onwards were first accumulated and then summed up monthly to compare with the model simulation outputs.

5.4.3.3 Stand density management diagram (SDMD) development

Forest stand density manipulation can affect forest growth and carbon storage. For a given stage in stand development, forest yield and biomass will continue to increase with increasing site occupancy until an asymptote occurs (Assmann, 1970). Consequently, applying the manipulation occupancy strategy rationally throughout harvesting via thinning management can result in maximum forest production and carbon sequestration (Drew and Flewelling, 1979; Newton, 2006). It should be conceptually identical to develop a carbon SDMD (CSDMD) and a volume SDMD (VSDMD) in terms of theories, approaches, and processes. Firstly, the relationship between volume and density was derived from the -3/2 power law (Eq. 2) (Yoda et al, 1963).

$$V = 10^{k} * N^{-3/2} \quad (2)$$

where V and N are stand volume (m^3/ha) and density (stems/ha), respectively. The constant parameter was estimated (k = 6.79) based on the simulated mean volume and the density of black spruce within the study area.

The reciprocal equation of the competition-density effect (Eq. 3) was then employed to

determine the isoline of the mean height (Kira et al, 1953; Hutchings and Budd, 1981).

$$1/v = a * H^b + c * H^d / N \quad (3)$$

where H is the mean height (m), and a, b, c, and d are the regression coefficients to be estimated.

Two other equations concerning the isoline of the mean diameter and self-thinning were used to carry out VSDMD.

Isoline of mean diameter:

$$V = a * D^b * N^c \quad (4)$$

Isoline of self-thinning:

$$V = a * (1 - N / N_0) * N_0^b \quad (5)$$

where D, N, and N_0 represent the mean diameter at breast height (cm), density, and initial density (stems/ha), respectively.

5.5. RESULTS

5.5.1 Model validation

Tree height and DBH are essential forest inventory measurements used to estimate timber volume and are also important variables for forest growth and yield modeling. To test model accuracy, simulated measurements were compared with averaged measurements of height and DBH in Chibougamau, Québec. Comparisons between height and DBH predicted by TRIPLEX with data collected through fieldwork were in agreement. The coefficient of determination (R^2) was approximately 0.94 for height and 0.93 for DBH (Fig. 5.3). Although forest inventory stands were estimated to be approximately 100 years old, increment cores taken at breast height analysis had less than 80 rings. As a result, Fig. 3 only presents 80-year-old forest stand variables within the simulation to compare with field measurements of height and DBH.

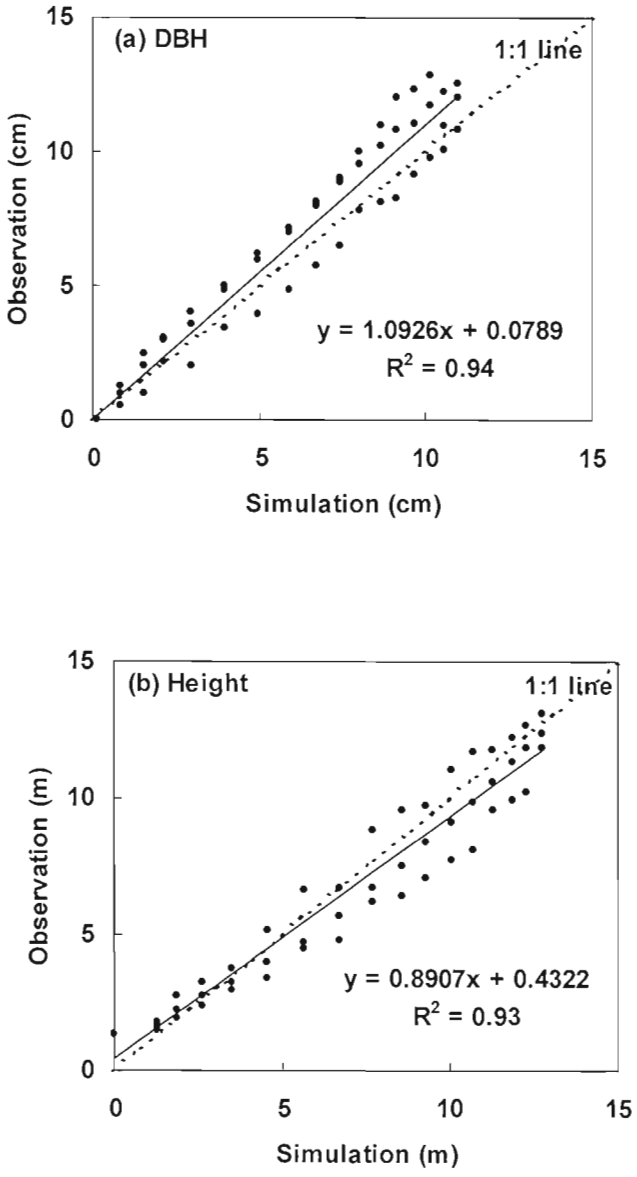

Fig. 5.3. Comparisons of mean tree height and diameter at breast height (DBH) between the TRIPLEX simulations and observations taken from the sample plots in Chibougamau, Québec, Canada.

Being the net carbon balance between the forest ecosystem and the atmosphere, NEP can indicate annual carbon storage within the ecosystem under study. The CCP-FCRN program has provided reliable and consecutive NEP measurements since 2003 by using an eddy covariance (EC) technique. Fig. 5.4 shows NEP comparisons between the TRIPLEX simulation and EC measurements taken from January, 2004, to December, 2007. Agreement for this period of time is acceptable overall ($R^2 = 0.71$).

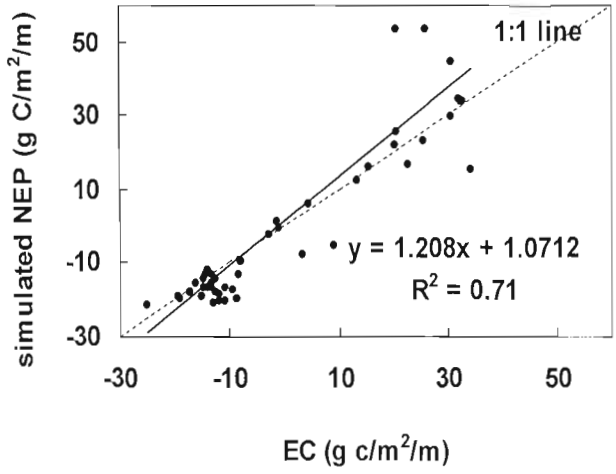

Fig. 5.4. Comparison of monthly net ecosystem productivity (NEP) simulated by TRIPLEX, including eddy covariance (EC) flux tower measurements from 2004 to 2007.

From the standpoint of growth patterns, the growth patterns and competition capacity of trees (including both interspecific and intraspecific competition) within the forest stands under study are the result of carbon allocation to the component parts of trees. Since the simulation was in agreement with field measurements for forest growth, net primary productivity (NPP) and its allocation to stem growth seem acceptable. This indicates that significant errors derive from heterotrophic respiration. The current algorithms established within the soil carbon and nitrogen submodel and the soil water submodel may, therefore, require further improvement.

5.5.2. Forest dynamics

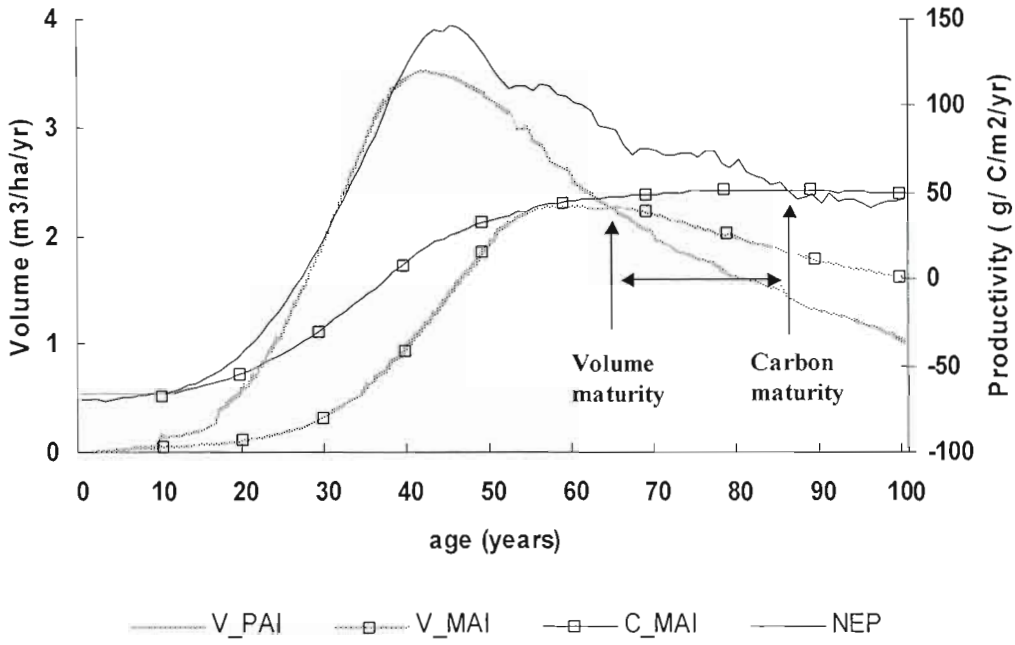

Fig. 5.5. Dynamics of the tree volume increment throughout stand development. Harvest time should be postponed by approximately 20 years to maximize forest carbon productivity. V_PAI: the periodic annual increment of volume (m3/ha/yr); V_MAI: the mean annual increment of volume (m3/ha/yr); C_MAI: the mean annual increment of carbon productivity (g/C/m2/yr); NEP: the annual net ecosystem productivity; and C_PAI: the periodic annual increment of carbon productivity (m3/ha/yr).

Increment is a quantitative description for a change in size or mass in a specified time interval as a result of forest growth. The annual forest volume increment and the annual change in carbon storage within the ecosystem over a one year period are illustrated in Fig.5.5. The periodic annual increment (V_PAI) increased rapidly for forest volume and then reached a maximum value (3.5m^3/ha/year) at approximately 43

years old. V_PAI dropped off quickly after this period. In comparison, the mean annual increment of volume (V_MAI) was small to begin with and then increased to a maximum at approximately 68 years old, at the point of intersection of the two curves. Beyond this intersection, V_MAI declined gradually but at a rate slower than V_CAI.

5.5.3. Carbon change

The forest ecosystem under examination for this study took approximately 40 years to switch from a carbon source to a carbon sink. NEP represents the annual carbon storage and can therefore be regarded as the periodic annual carbon increment (C_PAI). In contrast, the mean annual carbon increment (C_MAI) was derived by dividing the total forest carbon storage at any point in time by total age. Results indicate that the changing trend between annual carbon storage and volume increment was basically identical (Fig. 5.5). Both C_PAI and C_MAI, however, required longer periods to attain maximums at 47 and 87 years old, respectively. If the age of maximum V_MAI typically refers to the traditional quantitative maturity age (or optimum volume rotation age) due to the maximum total woody biomass production from a perpetual series of rotations (Avery and Burkhart, 2002), the point of intersection where C_MAI and C_PAI meet can be appointed the carbon maturity age (or optimum carbon rotation age) where the maximum amount of carbon can be sequestered from the atmosphere. Results here suggest that the established rotation age should be delayed by approximately 20 years to allow forests to reach the age of carbon maturity where they can store the maximum amount of carbon possible.

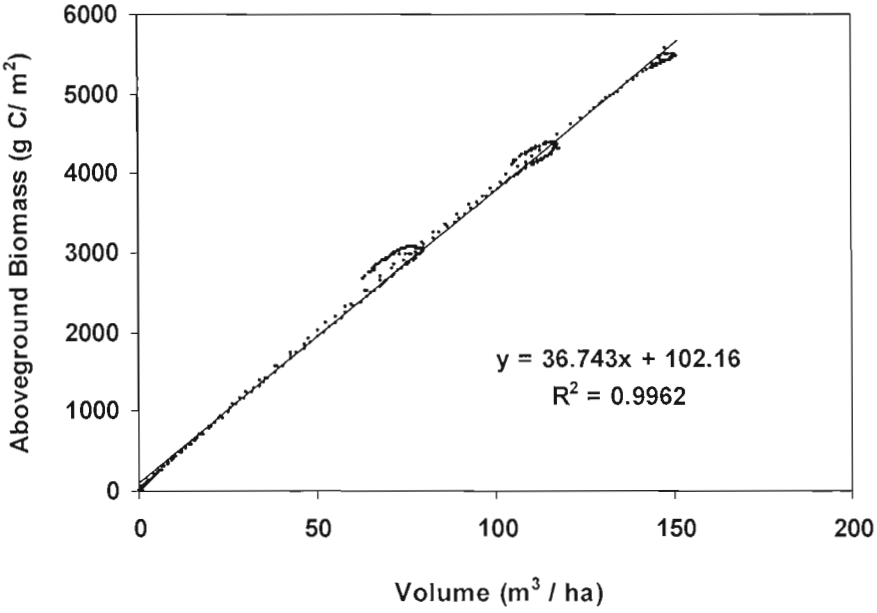

Fig. 5.6. Aboveground biomass carbon (g/C/m2) plotted against mean volume (m3/ha) for black spruce forests located near Chibougamau, Québec, Canada.

5.5.4. Stand density management diagram (SDMD)

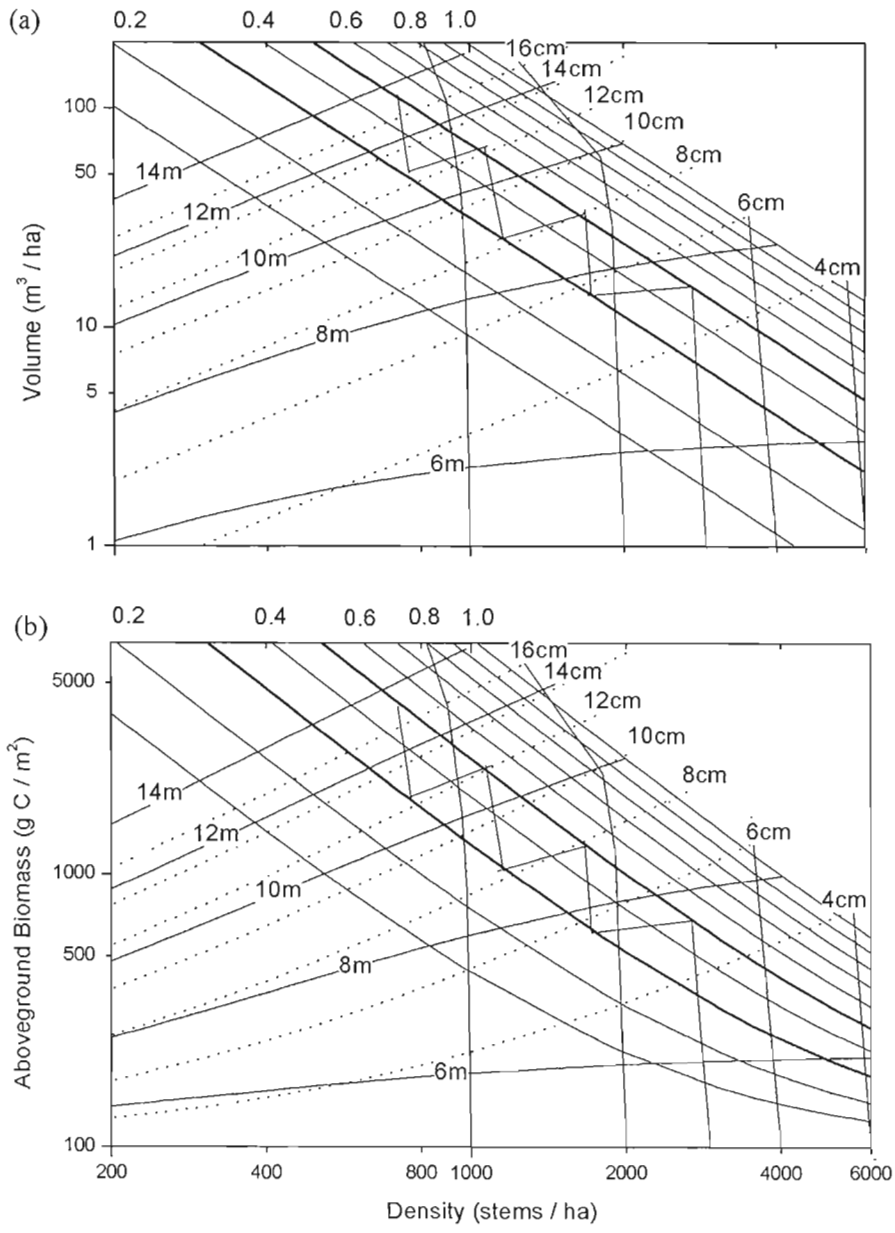

Fig. 5.7. Black spruce stand density management diagrams with log10 axes in Origin 8.0 for (a) volume (m3/ha) and (b) aboveground biomass carbon (g/C/m2), including crown closure isolines (0.13-1.0), mean diameter (cm), mean height (m), and a self-thinning line with a density of 1000, 2000, 4000, and 6000 (stems/ha), respectively.

Initial density (3000 stems/ha) is the sample used for thinning management to yield more volume and uptake more carbon.

Nonlinear regression coefficient results (Eq. 3 to 5) are provided for in Table 5.2. Fig. 5.6 indicates that tree volume was highly correlated to carbon storage (R^2 = 0.99). Black spruce VSDMD and CSDMD were developed based on these equations and the relationship between volume and aboveground biomass. Crown closure, mean diameter, mean height, and self-thinning isolines within a bivariate graph in which volume or carbon storage is represented on the ordinate axis and stand density is represented on the abscissa were graphically illustrated (Fig. 5.7a and b). Within these graphs, relationships between volume and carbon storage and stand density were expressed quantitatively at various stages of stand development. Results indicate that volume and abovegroundbiomass decrease with an increase in stand density and a decrease in site quality.

Table 5.2. Coefficients of nonlinear regression of all three equations for black spruce forest SDMD development.

Eqs.	A	b	c	d	R^2
(3)	516742.85	-8.04	116553.56	-3.85	0.92
(4)	0.0001	2.63	0.98		0.96
(5)	386952.56	-0.85			0.77

5.6. DISCUSSION

A realistic method to test ecological models and verify model simulation results is to evaluate model outputs related to forest growth and yield stand variables, which can be measured quickly and expediently for larger sample sizes. TRIPLEX was selected as the best-suited simulation tool due to its strong performance in describing growth and yield stand variables of boreal forest stands. TRIPLEX was designed to be applied at

both stand and landscape scales while ignoring understory vegetation that could result in under-estimation (Trumbore & Harden, 1997). This is a possible explanation why modeled results related to volume and biomass in this study was lower than results obtained by Newton (Newton, 2006). Additionally, the present study focused on a location in the northern boreal region where forests tend to grow more slowly with comparatively shorter growing seasons and low productivity. For example, observations by Valentini et al (2000) also showed a significant increase in carbon uptake with decreasing latitude, although gross primary production (GPP) appears to be independent of latitude. Their results also suggest that ecosystem respiration in itself largely determines the net ecosystem carbon balance within European forests.

The current study proposes that carbon exchange is a more determining factor overall than other variables, and it would be advantageous in regard to forest managerial practices for stakeholders to understand this fact. Results indicate that current harvesting practices that take place when forests reach maturity age may not, in fact, be the optimum rotation age for carbon storage. Two separate ages of maturity (volume maturity and carbon maturity) have been discovered for black spruce stands in eastern Canada (Fig. 5.5). Although a linear relationship exists between tree volume and aboveground carbon storage (Fig. 5.6), both variables possess different harvesting regimes decided on rotation age. The point in time between the mean annual increment of productivity (C_MAI) and the current annual increment of productivity (i.e., ANEP) takes place approximately 20 years later than that between the current annual increment of volume (V_CAI) and the mean annual increment of volume (V_MAI). In other words, the optimum age for harvesting to take place (the carbon maturity age) where maximum carbon sequestration occurs should be implemented 20 years after the rotation age where maximum volume yield occurs.

Fig. 5.5 illustrates that both the current annual increment of productivity (ANEP) and the current annual increment of volume (V_CAI) reaches a peak at the same age class. The former, however, decreases at a slower rate than the latter after this peak occurs. This is partly due to how changes in litterfall and heterotrophic respiration affect NEP

dynamics. The simulation carried out for this study did not detect any notable change in heterotrophic respiration following the point at which the peak occurred. However, litterfall greatly increases up until the age class of 70 years (Sharma and Ambasht, 1987; Lebret et al, 2001). The analysis of stand density management diagrams (SDMD) also supports this reasoning, comparing volume yield and carbon storage only for aboveground components (Fig. 5.7). A few differences do exist between the two SDMDs in terms of volume yield and aboveground carbon storage. Moreover, the age difference of the current annual increment of productivity (ANEP) and the current annual increment of volume (V_CAI) shown in Fig. 5.5 may be due to underground processes.

If scheduled correctly, thinning can increase total stand volume and carbon yield since it accelerates the growth of the remaining trees by removing immature stems and reducing overall competition (Drew and Flewelling, 1979; Hoover and Stout, 2007). Previous research has indicated that the relative density index should be maintained between 0.3 and 0.5 in order to maximize forest growth (Long, 1985; Newton, 2006).

Table 5.3. Change in stand density, diameter at breast height (DBH), volume, and aboveground carbon before and after thinning.

	Density (stems/ha)		DBH (cm)		Volume (m^3/ha)		Carbon (g C/m^2)	
Thinning								
	Before	After	Before	After	Before	After	Before	After
I	2800	1800	5.0	5.8	20	18	750	650
II	1800	1300	7.9	8.2	38	33	1500	1000
III	1300	800	12.0	12.4	60	48	3200	2800

A 3000 stems/ha initial density stand was simulated as an example of the thinning procedure (Fig. 5.6b). Initial thinning was carried out when the average height of the stand was close to 8m. Stand volume and aboveground carbon decreased immediately after thinning took place. However, the growth rate of the remaining trees increased as a result and in comparison to previous stands following the regular self-thinning line (see Fig. 5.6). Despite on the relative density line of 0.5, aboveground biomass carbon increased from 750g C/m^2 and up to 4000g C/m^2 after thinning was carried out twice more. Although stand density decreased by approximately 75%, mean DBH, height, and stand volume increased by an approximate factor of 3.4, 1.7, and 5.3, respectively. Table 5.3 provides detailed information (before and after thinning took place) of the three thinning treatments.

5.7. CONCLUSION

Forest carbon sequestration is receiving more attention than ever before due to the growing threat of global warming caused by increasing levels of anthropogenic fueled atmospheric CO_2. Rotation age and density management are important approaches for the improvement of silvicultural strategies to sequester a greater amount of carbon. After comparing conventional maturity age and carbon maturity age in relation to black spruce forests in eastern Canada, results suggest that it is premature in terms of carbon sequestration to harvest at the stage of biological maturity. Therefore, postponing harvesting by approximately 20 years to the time in which the forest reaches the age of carbon maturity may result in the formation of a larger carbon sink.

Due to the novel development of CSDMD, the relationship between stand density and carbon storage at various forest developmental stages has been quantified to a reasonable extent. With an increase in stand density and site class, volume and aboveground biomass increase accordingly. The increasing trend in aboveground biomass and volume is basically identical. Forest growth and carbon storage saturate when stand density approaches its limit. By thinning forest stands at the appropriate

stand developmental stage, tree growth can be accelerated and the age of carbon maturity can be delayed in order to enhance the carbon sequestration capacity of forests.

5.8. ACKNOWLEDGEMENTS

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CHAPTER VI

SYNTHESIS, GENERAL CONCLUSION, AND FUTURE DIECTION

6.1. MODEL DEVELOPMENT

Based on the two-leaf mechanistic modeling theory (Seller et al, 1996), in the Chapter II, a process-based carbon exchange model of TRIPLEX-FLUX has been developed with half hourly time step. As well, in Chapter V, the old version TRIPLEX with monthly time step has been updated and improved from big-leaf model to two-leaf model. In these two chapters, the general structures of model development were described. The model validation suggests that the TRIPLEX-Flux model is able to capture the diurnal variations and patterns of NEP for old black spruce in central Canada (Manitoba and Saskatchewan) (Fig. 2.3, Fig. 2.4, Fig. 3.2 and Fig.3.4) and mixedwood in Ontario (Fig.3.2 and Fig.3.3). A comparison with forest inventory and tower flux data demonstrates that the new version of TRIPLEX1.5 is able to simulate forest stand variables (mean height and diameter at breast height) and its carbon dynamics in boreal forest ecosystems of Quebec (Fig. 5.3 and Fig. 5.4).

Based on the sensitivity analysis reported in Chapter II (Fig. 2.5, Fig. 2.6, Fig. 2.7 and Fig.2.8), the relative role of different model parameters was recognized not to be the same in determining the dynamics of net ecosystem productivity. To reduce simulation uncertainties from spatial and seasonal heterogeneity, in Chapter IV, four key model parameters (m, V_{max}, J_{max}, and R_{10}) were optimized by data assimilation. The Markov Chain Monte Carlo (MCMC) simulation was carried out using the Metropolis-Hastings algorithm for seven carbon flux stations of North America Carbon Program (NACP). After parameter optimization, the prediction of net ecosystem production was improved by approximately 25% compared to CO_2 flux measurements measured (Fig.4.5).

6.2. MODEL APPLICATIONS

6.2.1. Mixedwood

Although both mixedwood and black spruce forests were acting as carbon sinks for the atmosphere during the growing season, the multi-species forest was observed to have a bigger potential to uptake more carbon (Fig. 3.5, Fig. 3.6 and Fig. 3.7). Mixedwood also presented several distinguishing features. First, the diurnal pattern was uneven, especially after completed leaf-out of deciduous species in June. Secondly, the response to solar radiation is stronger with superior photosynthetic efficiency and gross ecosystem productivity. Thirdly, carbon use efficiency and the ratio of NEP/GEP are higher.

Because of climate change impacts and natural disturbances (such as wildfire and insect outbreaks), the boreal forest distribution and composition could be changed. Some current single species coniferous ecoregions might be transformed into a mixedwood forest type, which would be beneficial to carbon sequestration. Whereas, switching mixedwood forests to pure deciduous forests may lead to reduced carbon storage potential, because the deciduous forests sequester even less carbon than pure coniferous forests (Bond-Lamberty et al., 2005). From the point of view of forest management, the mixedwood forest is suggested as a good option to extend and replace single species stands, which would enhance the carbon sequestration capacity of Canadian boreal forests, and, therefore, reduce atmospheric CO_2 concentration.

6.2.2. Management practice challenge

Rotation age and density management were suggested as important approaches for the improvement of silvicultural strategies to sequester a greater amount of carbon (IPCC, 1995, 1996). However, it is still currently a big challenge to use process-based models for forest management practices. To the best of my knowledge, this thesis is the first attempt to present the concept of carbon maturity and develop a management-oriented carbon stand density management diagram (CSDMD) at the stand level for black spruce forests in Canada. Previous studies by Newton et al., (2004, 2005) and Newton (2006) were based on the individual tree level and an empirical model, which is very difficult and complicated to scale up to a stand or landscape level using diameter distributions.

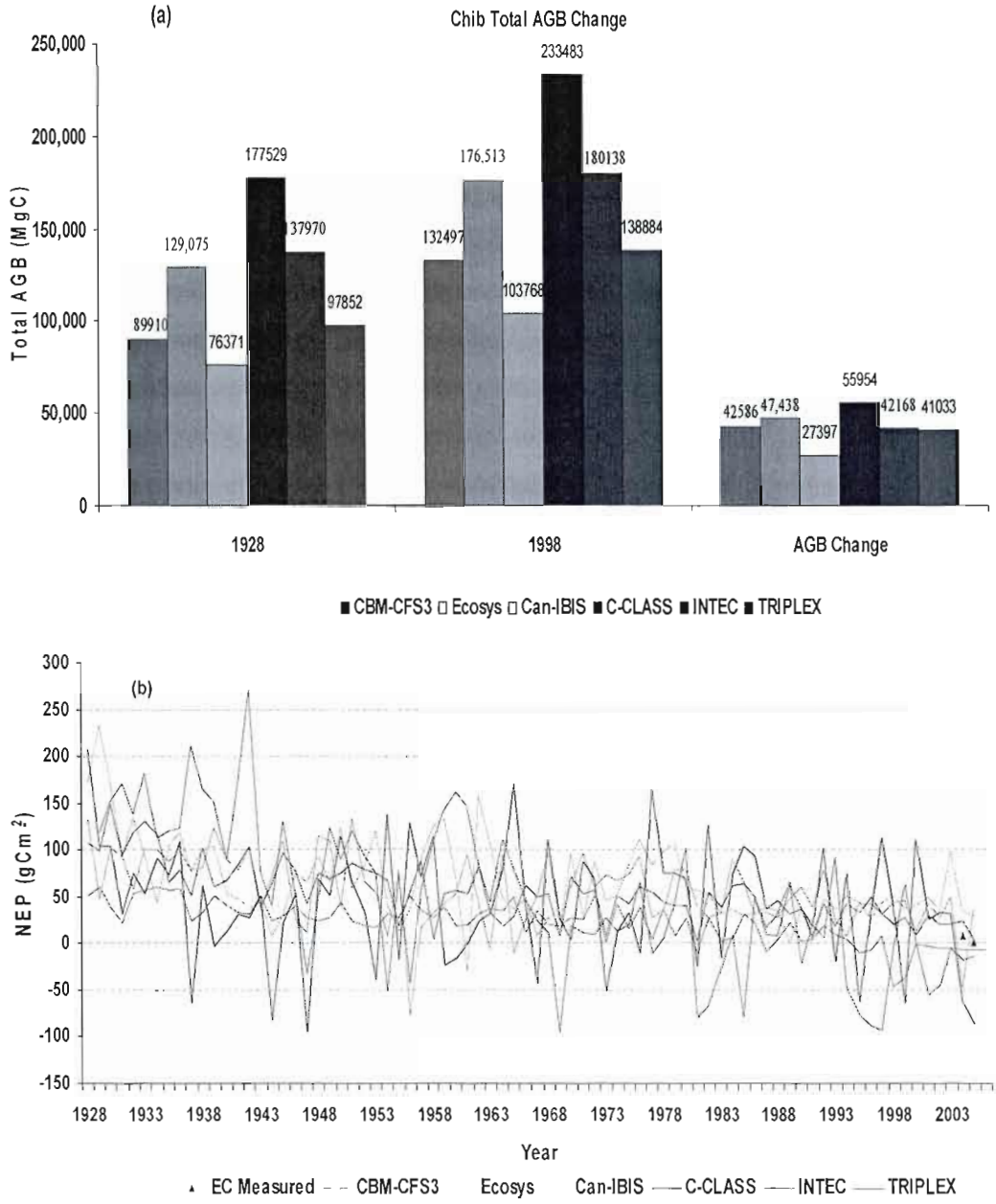
After comparing conventional maturity age and carbon maturity age in relation to black spruce forests in eastern Canada, the results reported in this thesis suggest that it is premature to harvest at the stage of biological maturity. Therefore, postponing harvesting by approximately 20 years to the time in which the forest reaches the age of carbon maturity may result in the formation of a larger carbon sink.

Owing to the novel development of CSDMD, the relationship between stand density and carbon storage at various forest developmental stages has been quantified to a reasonable extent. With an increase in stand density and site class, volume and aboveground biomass increase accordingly. The increasing trend in aboveground biomass and volume is basically identical. Forest growth and carbon storage saturate when stand density approaches its limit. By thinning forest stands at the appropriate stand developmental stage, tree growth can be accelerated and carbon maturity age can be delayed in order to enhance the carbon sequestration capacity of forests.

6.3. MODEL INTERCOMPARISON

The pioneer's studies showed the mid- and high-latitude forests in the Northern Hemisphere play major role to regulate global carbon cyle and have a significant effect on climate change (Wofsy et al, 1993; Dixon et al, 1994; Fan et al, 1998; Dixon et al, 1999). However, since the sensitivity to the climate change and the uncertainties to spatial and temporal heterogeneity, the results from empirical and process-based models are not consistent for Canadian forest carbon budgets (Kurz and Apps, 1999; Chen et al, 2000). The Canadian carbon program (CCP) recently initiated a Historical Carbon Model Intercomparison Project in which I was responsible for TRIPLEX model simulations. These intercomparisons were intended to provide an algorithm to incorporate weather effects on annual productivity in forest inventory models. We have performed a comparison exercise among 6 process-based models of forest growth (Can-IBIS, INTEC, ECOSYS, 3PG, TRIPLEX, CN-CLASS) and CBM-CFS3 as part of an effort to better capture inter-annual climate variability in the carbon accounting of Canada's forests. Comparisons were made on multi-decadal simulations for a Boreal

Black Spruce forest in Chibougamau (Quebec). Models were initiated using reconstructions of forest composition and biomass from 1928, followed by transition to current forest composition as derived from recent forest inventories. Forest management events and natural disturbances over the simulation period were provided as maps and disturbance impacts on a number of carbon pools were simulated using the same transfer coefficients parameters as CBM-CFS3. Simulations were conducted from 1928 to 1998 and final aboveground tree biomass in 1998 was also extracted from the independent forest inventory. Changes in tree biomass at Chibougamau were 10% less than estimates derived by difference between successive inventories. The source of this small simulation bias is attributable to the underlying growth and yield model, as well as to limitations of inventory methods. Overall, process-based models tracked changes in ecosystem C modeled by CBM-CFS3, but significant departures could be attributed to two possible causes. One was an apparent difficulty in reconciling the definition of various belowground carbon pools within the different models, leading to large differences in disturbance impacts on ecosystem C. The other was in the among-model variability in the magnitude and dynamics of specific ecosystem C fluxes such as gross primary productivity and ecosystem respiration. Agreement among process models about how temperature affects forest productivity at these sites indicates that this effect may be incorporated into inventory models used in national carbon accounting systems. In addition, from these preliminary results, we found that the TRIPLEX model as a hybrid model was able to take the advantages of both empirical and process-based models and provide reasonable simulation results (Fig. 6.1).



Modeling NEPs of grid cell 1869 within the fetch area during 1928-2005 and the EC measured NEPs during 2004-2005

Fig. 6.1. Model intercomparison (Adapt from Wang et al, CCP AGM, 2010).

6.4. MODEL UNCERTAINTY

6.4.1. Model Uncertainty

The previous studies (Clark et al., 2001; Larocque et al., 2008) have provided evidence that it is a big challenge to accurately estimate carbon exchanges within terrestrial ecosystems. Model prediction uncertainties stem primarily from the following five key factors including:

(1) Basic model structure: obviously, different models have different model structures, especially when comparing empirical models and process-based models. Actually, even among the process-based models, the time steps (e.g., hourly, daily, monthly, yearly) are different for each particular purpose.

(2) Initial conditions: for example, before simulation, some models (e.g., IBIS) need a long term running for the soil balance.

(3) Model parameters: since the model structures are different, different models need different parameters. Even with the same model, parameters should be changed for different ecosystems (e.g., boreal, temperate and tropical forest).

(4) Data input: since the model structures are different, different models need different information as input, for example weather, site, soil, time information.

(5) Natural and anthropogenic disturbance representation: due to lack of knowledge of ecosystem processes, disturbance effects on forest ecosystem are not well understood.

(6) Scaling exercises: some errors are derived from scaling (include both scaling-up and scaling-down) process.

Actually, during my thesis work, I became aware of other important limitations due to model uncertainty. For example, model validation suggests that TRIPLEX-Flux is able to capture the diurnal variations and patterns of NEP for old black spruce and mixedwood, but failed to simulate the peaks of NEP during the growing seasons (Fig. 2.2, Fig. 3.3 and Fig. 3.4). Previous studies have also provided evidence that it is a big challenge to accurately estimate carbon exchanges within terrestrial ecosystems. In the APPENDIX 1, dfferent sources of model uncertainty are synthesized. For the TRIPLEX, the prediction uncertainties should stem primarily from two aspects: soil and forest succession.

For long-term simulations, TRIPLEX shows encouraging results for forest growth. R^2 is 0.97 and 0.93 for height and DBH, respectively (Fig. 5.3). However, comparison with tower flux data, R^2 is 0.71. That means the main error is derived from heterotrophic respiration. However, no consensus has emerged on the sensitivity of soil respiration to environmental conditions due to the lack of data and feedback, which still remains largely unclear. In APPENDIX 2 and APPENDIX 3, a meta-analysis was introduced and applied as a means to investigate and understand the effects of climate change on soil respiration for forest ecosystems. The results showed that if soil temperature increased 4.8°C, soil respiration in forest ecosystems increased approximately 17% while soil moisture decreased by 16%. In the future, great efforts need to be made toward this direction in order to reveal the mystery and complicated soil process and their interactions, which is a new challenge and next step for carbon modeling.

Forest vegetation undergoes successional changes after disturbances (such as wildfire) (Johnson, 1992). In young stands, shade-tolerant species are poorly dispersed and grow more slowly than shade-intolerant species under ample light conditions (Greene et al, 2002). During stand development, shade-tolerant species reach the main forest canopy height and replace the shade-intolerant species. In order to better understand the impacts of climate change on forest composition change and its feedback in mixedwood forests over the time, a forest succession sub-model needs to be developed and used for simulating forest development process. Unfortunaltely, there is no forest successful submodel in the current TRIPLEX model. It seems that the LPJ-Guess model, a generalized ecosystem model to simulate vegetation structural and compositional dynamics under various disturbance regimes regimes and climate change (Smith et al, 2001), would be a good candidate for being incorporated into (or being coupled with) a future version of the TRIPLEX model in the near future.

6.4.2. Towards a Model-Data Fusion Approach and Carbon Forecasting

It is increasingly recognized that global carbon cycle research efforts require novel methods and strategies to combine process-based models and data in a systematic manner. This is leading research in the direction of the model-data fusion approach (Raupach et al., 2005; Wang et al., 2009). Model-data fusion is a new quantitative approach that provides a high level of empirical constraints on model predictions that are based upon observational data. A variety of computationally intensive data assimilation techniques have been recently applied to improve models within the context of ecological forecasting. Bayesian inversion, for example, has been a widely used approach for parameter estimation and uncertainty analysis for atmosphere-biosphere models. The Kalman filter is another method that combines sequential data and dynamic models to sequentially update forecasts. Hierarchical modeling provides a framework for synthesis of multiple sources of information from experiments, observations, and theory in a coherent fashion. Although these methods present powerful means for informing models with massive amounts of data, they are relatively new to ecological sciences, and approaches for extending the methods to forecasting carbon dynamics are relatively under-developed and/or under-utilized. In Chapter IV, only an optimization technique was used to estimate model parameters. Actually, this technique could be further applied to wider fields for further study, such as uncertainties and errors estimation, water and energy modeling, forecasting carbon sequestration, and so on. Fig.6.2 shows an overview of optimization techniques and model-data fusion application to ecological research.

In summary, the model-data fusion application by using inverse modeling and data assimilation techniques have great potential to enhance the capacity of vegetation and ecosystem carbon models to predict response of terrestrial forest and carbon cycling to a changing environment. In the upcoming data-rich era, the model-data fusion could help on improving our understanding of ecological process, estimating model parameters, testing ecological theory and hypotheses, quantifying and reducing model uncertainties, and forecasting changes in forest management regimes and carbon balance of Canadian boreal forest ecosystems.

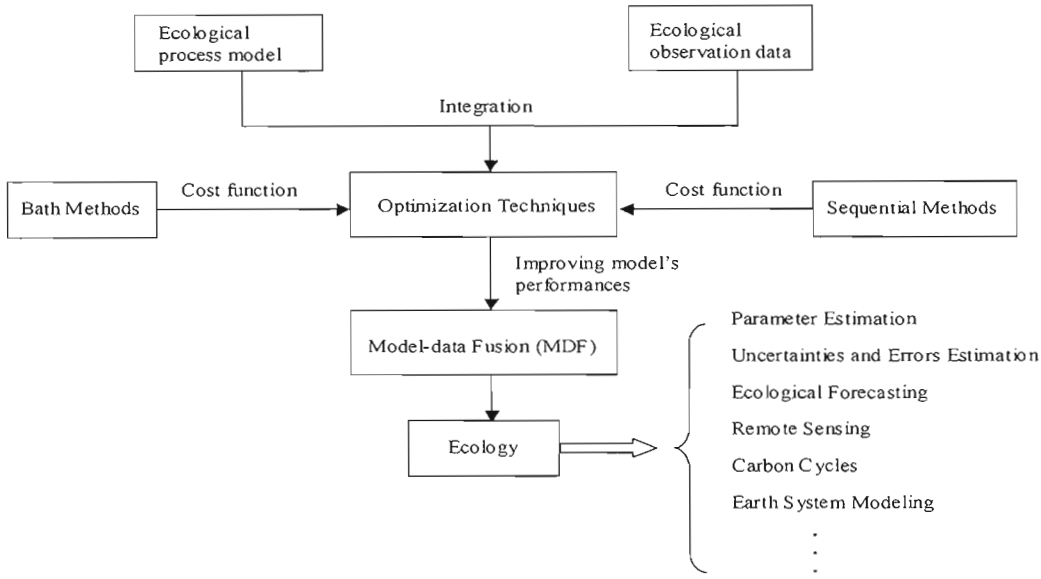


Fig. 6.2. Overview of optimization technique and model-data fusion application in ecology.

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APPENDIX 1

Uncertainty and Sensitivity Issues in Process-based Models of Carbon and Nitrogen Cycles in Terrestrial Ecosystems

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A.1. Introduction

Process-based models designed to simulate the dynamics of carbon (C) and nitrogen (N) cycles in northern forest ecosystems are increasingly being used in concert with other tools to predict the effects of environmental factors on forest productivity (Mickler et al., 2002; Peng et al., 2002; Sands and Landsberg, 2002; Almeida et al., 2004; Shaw et al., 2006) and forest-based C and N pools (Seely et al., 2002; Kurz and Apps, 1999; Karjalainen, 1996). Among the environmental factors, we include everything from intensive management practices to climate change, from local to global and from hours to centuries, respectively. Policy makers, including the general public, expect that reliable, well-calibrated and -documented processbased models will be at the centre of rational and sustainable forest management policies and planning as well as prioritisation of research efforts, especially those addressing issues of global change. In this context, it is important for policy makers to understand the validity of the model results and uncertainty associated with them (Chapters 2, 5 and 6). The term uncertainty refers simply to being unsure of something. In the case of a C and N model users are unsure about the model results. Regardless of a model's pedigree, there will always be some uncertainty associated with its output. The true values in this case can rarely if ever be determined and users need to assume the aberration between the model results and the true values as a result of uncertainties in the input factors as well as the process representation in the model. If it is also assumed that the model results are evaluated against measurements for which the true values are unknown because of measurement uncertainties, it is important to at least know the probability spaces for both measurements and model results in order to interpret the results correctly. All these uncertainties are ultimately related to a lack of knowledge about the system under study and measurement errors of their properties. It is necessary to communicate the process of uncertainty propagation from measurements to final output in order to make model results meaningful for decision support. Pizer (1999) explains that including uncertainty as opposed to ignoring it leads to significantly different conclusions in policymaking and encourages more stringent policy, which may result in welfare gains.

A.2. Uncertainty

Different sources of uncertainty are generally recognised in models of C and N cycles in forest ecosystems, and in biological and environmental models in general (O'Neill and Rust, 1979; Medlyn et al., 2005; Chapters 4–6):

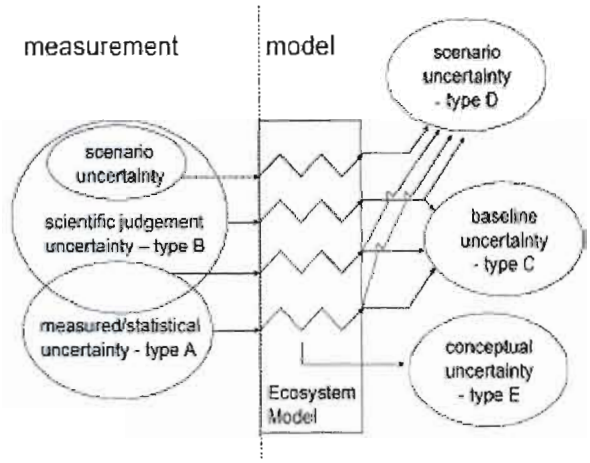

Figure A.1 Concept of uncertainty: the measurement uncertainty of type A and/or B are propagated through the model and leads to baseline uncertainty (type C) and scenario uncertainty (type D), where the propagation process is determined by the conceptual uncertainty (type E). (Adapted from Wattenbach et al., 2006.)

• data uncertainty associated with measurement errors, spatial or temporal scales or errors in estimates;

• model structure, and lack of understanding of the biological processes;

• the plasticity that is associated with estimating model parameters, due to the general interdependence of model variables and parameters; related to this is the search to determine the least set of independent variables required to span the most important system states and responses from one extreme to another, e.g. from frozen to non-frozen, dry to wet, hot to cold, calm to stormy;

• the range of variation associated with each biological system under study.

A.2.1 Uncertainty in measurements

The most comprehensive definition of uncertainty is given by the "Guide to express Uncertainties in Measurements – GUM" (ISO, 1995): "parameter, associated with the result of a measurement, that characterises the dispersion of the values that could reasonably be attributed to the measurand." The term parameter may be, for example, a standard deviation (or a given multiple of it), or the half-width of an interval having a stated level of confidence. In this case, uncertainty may be evaluated using a series of measurements and their associated variance (type A, Figure A.1) or can be expressed as standard deviation based on expert knowledge or by using all available sources (type B, Figure A.1). With respect to measurements, the GUM refers to the difference between error and uncertainty. Error refers to the imperfection of a measurement due to systematic or random effects in the process of measurement. The random component is caused by variance and can be reduced by an increased number of measurements. Similarly, the systematic component can also be reduced if it occurs from a recognisable process. The uncertainty in the result of a measurement on the other hand arises from the remaining variance in the random component and the uncertainties connected to the correction for system atic effects (ISO, 1995). If we speak about uncertainty in models it is very important to recognise this concept.

A.2.2 Model uncertainty

The definition of uncertainty in model results can be directly associated with the uncertainty of measurements. However, there are modelling-specific components we need to consider. First all models are by definition a simplification of the natural system. Thus uncertainty arises just from the way the model is conceptualised, which is defined as structural uncertainty. C and N models also use parameters in their equations. These internal parameters are associated with model uncertainty and they can have different sources, such as long-term experiments (e.g. decomposition constants for soil carbon pools) or laboratory experiments (temperature sensitivity of decomposition), defined as parameter uncertainty. Both uncertainties refer to the design of the model and can be summarised as conceptual uncertainty (type E, Figure

A.1) Models are highly dependent on input variables and parameters. Variables are changing over the runtime of a model whereas parameters are typically constant, describing the initialisation of the system. As both variables and parameters are model inputs, they are often called input factors in order to distinguish them from internal variables and parameters (Wattenbach et al., 2006).

If the data for input factors are determined by replicative measurements, they can be labelled according to the GUM as type A uncertainty. In many cases the set of type A uncertainty can be influenced by expert judgement (type B uncertainty), which results in the intersection of both sets (e.g. the gapfilling process of flux data is as such a type B uncertainty that influences type A uncertainty in measurements). A subset of type B uncertainty are scenarios. Scenarios (see Chapters 4 and 11) are assumptions of future developments based on expert judgement and incorporate the high uncertain element of future developments that cannot be predicted. If we use scenarios in our models, we need to consider them as a separate instance of uncertainty (type D, Figure A.1) because they incorporate all elements of uncertainty (Wattenbach et al., 2006).

Many methodologies have been used to better quantify the uncertainty of model parameters. Traditionally, these methodologies include simple trial-and-error calibrations, fitting model calculations with known field data using linear or non-linear regression techniques and assigning pre-determined parameter values, generated empirically through various means in the laboratory, the greenhouse or the field. For example, Wang et al. (2001) used non-linear inversion techniques to investigate the number of model parameters that can be resolved from measurements. Braswell et al. (2005) and Knorr and Kattge (2005) used a stochastic inversion technique to derive the probability density functions for the parameters of an ecosystem model from eddy covariance measurements of atmospheric C. Williams et al. (2005) used a time series analysis to reduce parameter uncertainty for the derivation of a simple C transformation model from repeated measurements of C pools and fluxes in a young ponderosa pine stand, and Dufrêne et al. (2005) used the Monte Carlo technique to

estimate uncertainty in net ecosystem exchange by randomly varying key parameters following a normal distribution.

Erroneous parameter assignments can lead to gross over- or under-predictions of forest-based C and N pools. For example, Laiho and Prescott (2004) pointed out that Zimmerman et al. (1995), using an incorrect C/N ratio (of 30) for coarse woody debris in the CENTURY (http://www.nrel.colostate.edu/projects/century/nrel.htm) model, greatly overestimated the capability of a forest system to retain N. Prescott et al. (2004) also suggested that models that do not parameterise litter chemistry in great detail may represent long-term rates of leaf litter decay better than those models which do. The success or failure of a model depends to a large extent on determining whether or not expected model outputs depend on particular values used for model compartment initialisation. Models that are structured to be conservative, by strictly following the rules of mass, energy and electrical charge conservation, and by describing transfer processes within the ecosystem by way of simple linear differential or difference equations, lead to an eventual steady-state solution within a constant input–output environment, regardless of the choice of initial conditions. The particular parameter values assigned to such models determine the rate at which the steady state is approached. One important way to test the proper functioning of model parameterisation and initialisation is to start the model calculations at steady state, and then impose a disturbance pulse, or a series of disturbance pulses (harvesting, fire events, spaced regularly or randomly). This is to see whether the ensuing model calculations will correspond to known system recovery responses, and whether these calculations will eventually return to the initial steady state. The empirical process formulation is crucial, in that each calculation step must feasibly remain within the physically defined solution space. For example, in the hydro-thermal context of C and nutrient cycling, this means that special attention needs to be given to how variations of "independent" variables, such as soil organic matter, texture, coarse fragment content, phase change (water to ice), soil density and wettability, combine deterministically and stochastically to affect subsequent variations in heat and soil moisture flow and retention (Balland and Arp, 2005).

A.2.2.1 Structural uncertainty

Process-based forest models vary from simple to complex, simulating many different process and feedback mechanisms by integrating ecosystem-based process information on the underlying processes in trees, soil and the atmosphere. Simple models often suffer from being too simplistic, but can nevertheless be illustrative and educational in terms of ecosystem thinking. They generally aim at quickly estimating the order of magnitude of C and N quantities associated with particular ecosystem processes, such as C and N uptake and stand-internal C and N allocations. Complex models can, in principle, reproduce the complex dynamics of forest ecosystems in detail. However, their complexity makes their use and evaluation difficult. There is a need to quantify output uncertainty and identify key parameters and variables. The uncertainties are linked: uncertain parameters imply uncertain predictions and uncertainty about the real world implies uncertainty about model structure and parameterisation. Because of these linkages, model parameterisation, uncertainty analysis, sensitivity analysis, prediction, testing and comparison with other models need to be based on a consistent quantification of uncertainty.

Process-based C and N models are generally referred to as being deterministic or stochastic. These models may be formulated for the steady state (for which inputs equal outputs), or the dynamic situation, where model outcomes depend on time, in relation to time-dependent variations of the model input, and in relation to state-dependent component responses. Models are either based on empirical or theoretical derivations, or a combination of both (semi-empirical considerations). Process-based modelling is cognisant of the importance of model structure: the number and type of model components are carefully chosen to mimic reality and to minimise the introduction of modelling uncertainties.

Many problems are generated by model structure alone. Two issues can be related to model structure: (1) mathematical representation of the processes and (2) description of state variables. For example, several types of models can be used to represent the effect of temperature variation on processes, including the Q10 model, the Arrhenius function

or other exponential relationships. The degree of uncertainty in the predictions of a model can increase significantly if the relationship representing the effect of temperature on processes is not based on accurate theoretical description (see Kätterer et al., 1998; Thornley and Cannell, 2001; Davidson and Janssens, 2006; Hill et al., 2006). Most C and N models contain a relatively simple representation of the processes governing soil C and N dynamics, including simplistic parameterisation of the partitioning of litter decomposition products between soil organic C and the atmosphere. For example, the description of the mineralisation (chemical, physical, and biological turnover) of C and N in forest ecosystems generally addresses three major steps: (1) splitting of the soil organic matter into different fractions, which decompose at different rates, (2) evaluating the robustness of the mineralisation coefficients of the adopted fractions, and (3) initialising the model in relation to the fractions (Wander, 2004).

Table A.1 gives a cross-section of a number of recent models (or subcomponents of models) used to determine litter decomposition rates. The entries in this table illustrate how the complexity of the C and N modelling approach varies, even in describing a basic process such as forest litter decomposition. The number of C and N components in each model ranged from 5 to 10. The number of processes considered varied from 5 to 32 and the number of C and N parameters ranged from 7 to 54. The number of additional parameters used for describing the N mineralisation process, once the organic matter decomposition process is defined, is particularly interesting; it ranged from 1 to 27.

Most soil C models use three state variables to represent different types of soil organic matter (SOM), the active, slow and passive pools. Even though it is assumed that each pool contains C compound types with about the same turnover rate, this approach remains nevertheless conceptual and merely represents an abstraction of reality, which may lead to uncertainty in the predictions (type E, Figure A.1) (Davidson and Janssens, 2006). Also, these conceptual pools do not directly correspond to measurable pools. In reality, SOM contains many types of complex compounds with very different turnover

Table A.1 Examples of models used for estimating rate of forest litter decomposition

Model name	Reference	Predicted variables	Initialization variables	Predictor variables	Compartment number	Compartment type	Flows	Parameters	Comments
SOMM	Chertov and Komarov (1997)	C and N remaining	Initial C, N, ash content	Annual, monthly or daily soil moisture and temperature estimates	3*x* C, 3*x* N; (*x* represents number of cohorts considered)	C & N litter, fermentation and humus cohorts (leaves, roots, coarse woody debris, etc.)	7C, 7N	58 C, 3N	Parameters common across locations, initialised by species (cohort); C/N ratios prescribed per compartment
CENTURY	Parton et al. (1987)	C and N remaining	Initial C, N, C/N ratios, lignin	Monthly precipitation and air temperature estimates	5 C, 5 N	Structural, metabolic, active, slow and passive C & N compartments	13 C, 13 N	20 C, 5 N	Parameters common across locations; initialised by species
CANDY	Franko et al. (1995)	C and N remaining	Initial C, N	Monthly or daily soil moisture and temperature estimates	3 C, 3 N	Active, metabolic and stable C & N compartments	3 C, 3 N	5 C, 1 N, + 2 climate parameters (differs from original)	Parameters common across locations; decomposition not species specific
DOC-MOD	Currie and Aber (1997)	C and N remaining; dissolved organic C and N	Initial C, N, by compartment	Annual actual evapotranspiration estimates	5 C, 5 N	Lignin-cellulose, unprotected cellulose, extractives, microbial and humus C & N compartments	11 C, 10 N	17 C, 4 N	Parameters common across locations; C/N of humus prescribed
FLDM	Zhang et al. (2007)	Mass, C and N remaining	Initial mass, C, N; initial ash and acid and non-acid hydrolysable fractions, or lignin fraction	January & July air temperatures and annual precipitation, by year; or monthly or daily soil moisture and temperature estimates	3 mass, 2 N	Fast C; slow and very slow C & N compartments	3 C, 2 N	11C, 1 N	Parameters common across locations; CIDET calibrated; C/N ratios process determined
DECOMP	Wallman et al. (2006)	CO_2, soluble compounds, C remaining	Mass, chemical constituents of the soil organic matter (e.g., lignin, holocellulose)	Soil temperature, soil moisture, field capacity, wilting point, potential evapotranspiration, precipitation	4 C, 1 soil solution	Cellulose, lignin easily decomposable and resistant C, cellulose, soil solution	9 C, 9 Water	24 C, 8 water	Very detailed description of the chemistry. Remains to be tested for different sites

rates and amplitude of reaction to change in temperature (Davidson and Janssens, 2006). There have been many attempts to find relations between model structure and the real world either by measuring different decomposition rates of different soil fractions (Zimmermann et al., 2007) or by restructuring the model pools (e.g. Fang et al., 2005).

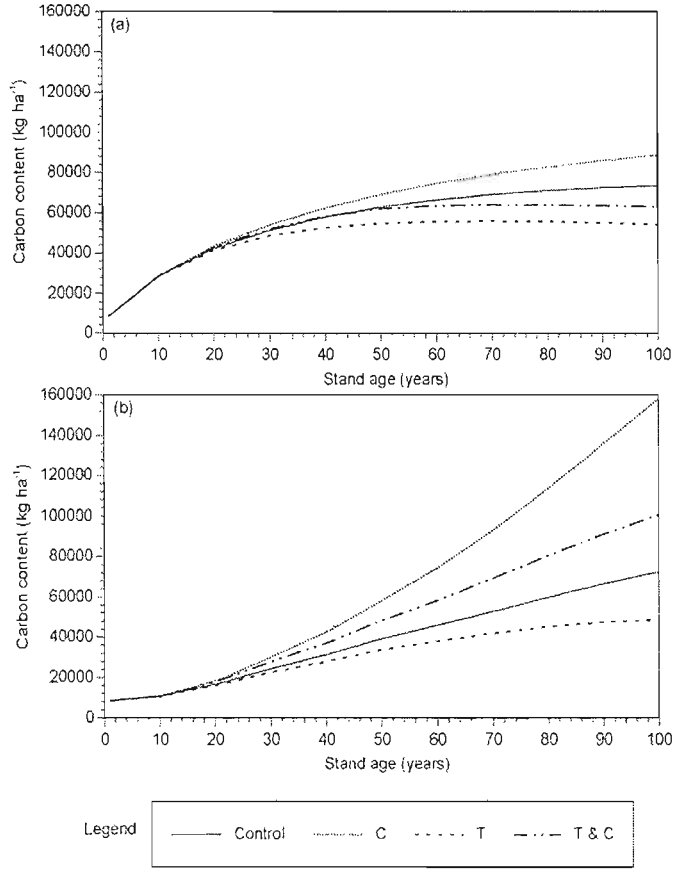

Figure A.2 Carbon content in stems, coarse roots and branches (large wood) predicted by CENTURY (a) and FOREST-BGC (b) under different scenarios of climate change based on CO2 increase from 350 to 700 ppm (C) and a gradual increase in temperature by 6.1 °C (T). The control includes the simulation results when the actual conditions remained unchanged. (Adapted from Luckai and Larocque, 2002, with kind permission of Springer Science and Business Media.)

Complex models have, in theory, the challenge of being more precise and/or accurate than simple models. This being so, data requirements for the initialisation and calibration of complex models need to be tightly controlled, and need to stay within the range of current field experimentation and exploration. The degree of model complexity also needs to be controlled, because this affects the overall model transparency and communicability, as well as affordability and practicality. Also, making models more complex can increase their structural uncertainty simply by increasing the number of parameters that are uncertain or affecting the correctness of the description of the processes involved.

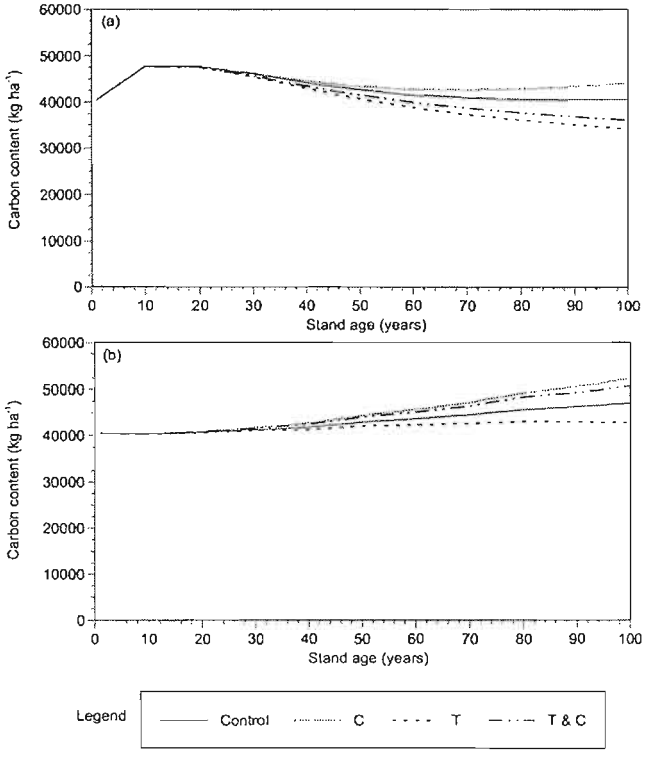

Figure A.3 Soil carbon content predicted by CENTURY (a) and FOREST-BGC (b) under different scenarios of climate change based on a CO2 increase from 350 to 700 ppm (C) and a gradual increase in temperature by 6.1 °C (T). The control includes the simulation results when the actual conditions remained unchanged. (Adapted from Luckai and Larocque, 2002, with kind permission of Springer Science and Business Media.)

This can be illustrated by a study conducted by Luckai and Larocque (2002), who compared two complex process-based models, CENTURY and FORESTBGC, to predict the effect of climate change on C pools in a black spruce (*Picea mariana* [Mill.] B.S.P.) forest ecosystem in northwestern Ontario (Figures A.2 and 18.3). For the prediction of the long-term change in C content in the large wood and soil pools, both models predicted relatively close carbon content under scenarios of actual climatic conditions and a gradual increase in temperature, even though the pattern of change differed slightly. Substantial differences in C content were obtained when two scenarios of CO2 increase were simulated. For the effect of gradual CO2 increase (actual temperature conditions remained unchanged), both models predicted increases in C content relative to actual temperature conditions. However, the increase in large wood C content predicted by FOREST-BGC was far larger than the increase predicted by CENTURY. The scenario that consisted of a gradual increase in both CO2 and temperature resulted in widely different patterns. While CENTURY predicted a relatively small decrease in large wood and soil C content, FOREST-BGC predicted an increase. The discrepancies in the results can be explained by differences in the structure of both models. Both models include a description of the above- and below-ground C dynamics. However, CENTURY focuses on the dynamics of litter and soil carbon mineralisation and nutrient cycling and FOREST-BGC is based on relatively detailed descriptions of ecophysiological processes, including photosynthesis and respiration. For instance, CENTURY considers several soil carbon pools (active, slow and passive) with specific decomposition rates, while FOREST-BGC considers one carbon pool. Both models also differ in input data. For instance, while CENTURY requires monthly climatic data, FOREST-BGC uses daily climatic data.

Modellers must carefully consider the tradeoff between the potential uncertainty that may result from adding additional variables and parameters and the gain in accuracy or precision by doing so. It may be argued as well that existing models of the C cycle are still in their infancy. It is not evident that modellers involved in the development of

process-based models have considered all the tools, including mathematical development, systems analysis and programming, to deal with this complexity.

A.2.2.2 Input data uncertainties and natural variation

Data uncertainties are linked to:

• The high spatial and temporal variations associated with forest soil organic matter and the corresponding dynamics of above- and below-ground C and N pools. For example, Johnson et al. (2002) noted that soil C measurements from a controlled multi-site harvesting study were highly variable within sites following harvest, but that there was little lasting effect of this variability after 15–16 years.

• Determining the parameters needed to define pools and fluxes (e.g. forest and vegetation type, climate, soil, productivity, and allocation transfers), and knowing whether these parameters are truly time and/or state-independent. Calibration parameters are, as a rule, fixed within models. They are usually obtained from other models, derived from theoretical considerations or estimated from the product of combinatorial exercises.

• Data definitions, sampling procedures, especially those that are vague and open to interpretation, and measurement errors. For example, Gijsman et al. (2002) discussed an existing metadata confusion about determining soil moisture retention in relation to soil bulk density.

• Inadequate sampling strategies, in the context of capturing existing micro- and macro-scale C and N pool variations within forest stands, and across the landscape, at different times of the year. On a regional scale, failure to account for the spatial variation across the landscape, and the vertical variation with horizon depth (due to microrelief, animal activity, windthrow, litter and coarse woody debris input, human activity and the effect of individual plants on soil microclimate and precipitation chemistry), may lead to uncertainty.

• Knowing how errors propagate through the model calculations. For example, soil C and N estimates of individual pedons are generally determined by the combination of measurements of C and N concentrations, soil bulk density, soil depth, and rock

content (Homann et al., 1995); errors in any one of these add to the overall estimation uncertainties.

By definition, process-based models should be capable of reflecting the range of variation that exists in ecosystems of interest. This is an important issue in forest management. In boreal forest ecosystems, quantifying the range of variation has become a practical goal because forest managers must provide evidence that justifies their proposed use of silviculture (e.g. harvesting, planting, tending) as a stand replacing agent. The range of variation has been defined by Landres et al. (1999) as "the ecological conditions, and the spatial and temporal variation in these conditions, that are relatively unaffected by people within a period of time and geographical area to an expressed goal." Assuming that reasonable boundaries of time period, geography and anthropogenic influence can be identified, the manager or scientist must then decide which metrics will be used to quantify the range of variation. Common metrics include mean, median, standard deviation, skewness, frequency, spatial arrangement and size and shape distributions (Landres et al., 1999). The adoption of the range of variation as a guiding principal of forest resource management is well-suited to boreal systems because (1) large, stand replacement natural disturbances continue to dominate in much of the boreal forest and (2) such disturbances may be reasonably emulated by forest harvesting (Haeussler and Kneeshaw, 2003).

The boreal forest is a region where climate change is predicted to significantly affect the survival and growth of native species. Consequently, policies and social pressures (e.g. Kyoto Protocol, Certification) may intensify efforts to improve forest C sequestration by reducing "low-value" wood harvesting. However, high prices for crude oil and loss of traditional pulp and paper wood markets may do the opposite by identifying "low-value" forest biomass as a readily available and profitable energy source. Quantifying the range of variation therefore becomes practical as companies and communities responsible for forest management have the obligation to provide evidence to justify proposed choices and use of harvesting/silviculture as stand-replacing procedures. However, including variables that account for the range of

variation increases the number and costs of required model calibrations, even for simple C and N models.

Structurally, process-based models often include a choice for the user – "stochastic or mean values." Stochastic runs usually require an estimate of the variation in some aspect of the system of interest. For example, CENTURY has a series of parameters that describe the standard deviation and skewness values for monthly precipitation as main drivers of ecosystem process calculations. This allows the model to vary precipitation, but not air temperature. Another option in CENTURY allows the user to write weather files that provide monthly values for temperature and precipitation. However, neither of these options allows for stochasticity in stand replacing events that subsequently affect drivers, such as moisture or temperature, and processes, such as decomposition or photosynthesis.

From a philosophical point of view, it makes sense to build the range of variation into model function. Boreal systems are highly stochastic, the evidence of which can be found in the high level of beta and gamma diversity often reported. From a logistic point of view, however, including variables that account for the range of variation increases the number of required calibration values and subsequently the cost of calibrating even a simple model. Data describing the range of variation is itself hard to come by. An operational definition of the range of variation is therefore needed, but has not been widely adopted (Ride, 2004).

A.2.3 Scenario uncertainty and scaling

Models are used at very different temporal and spatial scales, e.g. from daily to monthly to annual, and from stand- to catchment- to landscape-levels (Wu et al., 2005). The change in scales in model and input data introduces different levels of uncertainty. Natural variation is scale-dependent. For example, at the landscape level, it may be possible to: (1) estimate the range of stand compositions and ages, and therefore of structures; (2) determine a reasonable range of climatic conditions (mainly minimum and maximum temperatures and precipitation) for timeframes as long as a few

rotations (i.e. several hundred years); and (3) identify the successional pathways that reflect the interaction of (1) and (2). This information could then be used to provide a framework of stand and weather descriptions within which functional characteristics, such as SOM turnover, growth, and nutrient cycling, could be modelled. Assuming that we have reasonable mathematical descriptions of key biological, chemical, and physical processes – such as photosynthesis and decomposition, weathering and complexation, soil moisture, and compaction – we could then "nest" our models one inside of another. This approach assumes that the range of variation in the pools and fluxes normally included in process-based models is externally driven (i.e. by weather or disturbance) rather than by internal dynamics.

One example of such a model dealing with the range of variation in scaling issues is the General Ensemble Biogeochemical Modelling System (GEMS), which is used to upscale C and N dynamics from sites to large areas, with associated uncertainty measures (Reiners et al., 2002; Liu et al., 2004a, 2004b; Tan et al., 2005; Liu et al., 2006). GEMS consists of three major components: one or multiple encapsulated ecosystem biogeochemical models, an automated model parameterisation system, and an input/output processor. Plot-scale models such as CENTURY (Parton et al., 1987) and EDCM (Liu et al., 2003) can be encapsulated in GEMS. GEMS uses an ensemble stochastic modelling approach to incorporate the uncertainty and variation in the input databases. Input values for each model run are sampled from their corresponding range of variation spaces, usually described by their statistical information (e.g. moments, distribution). This ensemble approach enables GEMS to quantify the propagation and transformation of uncertainties from inputs to outputs. The expectation and standard error of the model output are given as:

$$E[p(X_i)] = \frac{1}{W}\sum_{j=1}^{w} p(X_{ij}),$$

$$S_E = \sqrt{\frac{V[p(X_i)]}{W}} = \sqrt{\frac{\frac{1}{W-1}\sum_{j=1}^{w}(p(X_{ij}) - E[p(X_i)])^2}{W}}.$$

where W is the number of ensemble model runs, and Xij is the vector of EDCM model input values for the j th simulation of the spatial stratum i in the study area, p is a

model operator (e.g. CENTURY or EDCM), and E, V, and SE are the expectation, variance, and standard error of model ensemble simulations for stratum i, respectively.

A.3. Model Validation

Model validation is an additional source of uncertainty as, among other mechanisms, it compares model results with measurements, which are again associated with uncertainties. Thus the choice of the validation database determines the accuracy of the model in further ad hoc applications. However, model validation remains a subject of debate and is often used interchangeably with verification (Rykiel, 1996). Rykiel (1996) differentiated both terms by defining verification as the process of demonstrating the consistency of the logical structure of a model and validation as the process of examining the degree to which a model is accurate relative to the goals desired with respect to its usefulness. Validation therefore does not necessarily consist of demonstrating the logical consistency of causal relationships underlying a model (Oreskes et al., 1994). Other authors have argued that validation can never be fully achieved. This is because models, like scientific hypotheses, can only be falsified, not proven, and so the more neutral term "evaluation" has been promoted for the process of testing the accuracy of a model's predictions (Smith et al., 1997; Chapter 2). Although model validation can take many forms or include many steps (e.g. Rykiel, 1996; Jakeman et al., 2006), the method that is most commonly used involves comparing predictions with statistically independent observations. Using both types of data, statistical tests can be performed or indices can be computed. Smith et al. (1997) and Van Gadow and Hui (1999) provide a summary of the indices most commonly used:

$$\text{mean residual} = \left(\sum (y_i - \hat{y}_i)/n\right),$$

$$\text{root mean square error} = \left(\sqrt{\sum (y_i - \hat{y}_i)^2/n - 1 - p}\right),$$

$$\text{model efficiency} = \left(\sum (y_i - \hat{y}_i)^2 / \sum (y_i - \bar{y}_i)^2\right),$$

$$\text{variance ratio} = \sum (\hat{y}_i - \bar{\hat{y}}_i)^2 / \sum (y_i - \bar{y}_i)^2.$$

Several examples of the comparison of predictions with observations or field determinations exist in the literature (Smith et al., 1997; Morales et al., 2005). However, these mostly involve traditional empirical growth models in forestry as part of the procedures used to determine the annual allowable cut within specific forest management units (e.g. Canavan and Ramm, 2000; Smith-Mateja and Ramm, 2002; Lacerte et al., 2004). In contrast, reports on a systematic validation of C and N cycle models are rare (e.g. De Vries et al., 1995; Smith et al., 1997) and needed. The validation of C and N cycle models based on the comparison of predictions and observations has been more problematic than the validation of traditional empirical growth and yield models. Long-term growth and yield data are available for the latter because forest inventories, including permanent sample plots with repeated measurements, have been conducted by government forest agencies or private industry for many decades. Therefore, process-based model testing has been largely based on growth variables, such as annual volume increment (Medlyn et al., 2005). Although volumetric data can be converted to biomass and C, direct measurements of C and N pools and flows in forest ecosystems have been collected mainly for research purposes and historical datasets are relatively rare. Therefore, it is often difficult to conduct a validation exercise of C and N models based on the comparison of predictions with statistically independent observations.

So, what options exist for the validation of forest-based C and N cycle models? The most logical avenue is the establishment and maintenance of long-term ecological research programs and site installations to generate the data needed for both model formulation and validation. However, these remain extremely costly and do not receive much political favour in this day and age. One alternative consists in using short-term physiological process measurements (e.g. Davi et al., 2005; Medlyn et al., 2005; Yuste et al., 2005), although careful scrutiny should be given to the long-term behaviour of the models in predicting C stocks in vegetation and soils (e.g. Braswell et al., 2005). Recent technological advances in micrometeorological and physiological instrumentation have been significant, such that it is now possible to collect and analyse hourly, daily, weekly or seasonal data under a variety of forest cover types,

experimental scenarios and environmental conditions at relatively low cost. The data from flux tower studies are just now becoming extensive enough to capture the broad spectrum of climatic and biophysical factors that control the C, water and energy cycles of forest ecosystems. The fundamental value of these measurements derives from their ability to provide multi-annual time series at 30-minute intervals of: the net exchanges of CO2, water, and energy between a given ecosystem and the atmosphere at a spatial scale that typically ranges between 0.5 and 1 km2. The two major component processes of the net flux (i.e. ecosystem photosynthesis and respiration) are being collected. Since different ecosystem components can respond differently to climate, multi-annual time series combined with ecosystem component measurements are carried out to separate the responses to inter-annual climate variability. These data are essential for development and validation of process-based models that could be a key part of an integrated C monitoring and prediction system. For example, Medlyn et al. (2005) validated a model of CO2 exchange using eddy covariance data. Davi et al. (2005) also used data from eddy covariance measurements for the validation of their C and water model, and closely monitored branch and leaf photosynthesis, soil respiration, and sap flow measurement throughout the growing season for additional validation purposes. The age factor, the effect of which takes so long to study, can be integrated by using a chrono-sequence approach (using stands of different ages on similar sites as a surrogate for time), which deals with validating C and N models by comparing model output with C and N levels and processes in differently aged forest stands of the same general site conditions. There is also the need to develop new methodologies that are able to integrate the above approaches to allow for model validation at fine and coarse time resolution.

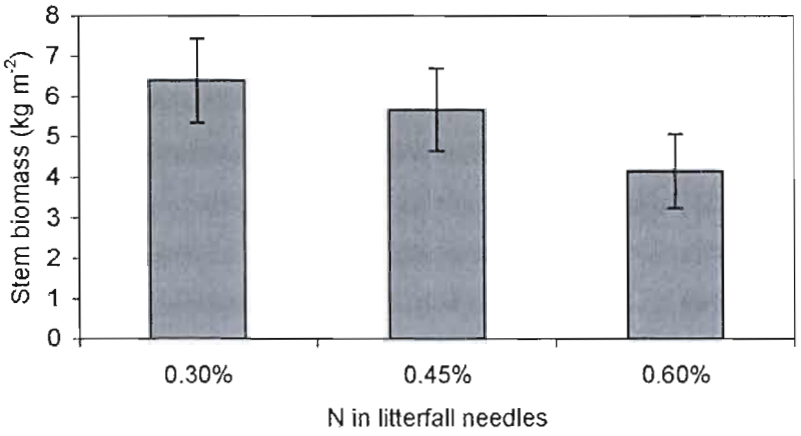

Figure A.4 Sensitivity of simulated stem biomass to N content in needles after abscission.

A.4. Sensitivity Analysis

Sensitivity analysis consists in analysing differences in model response to changes in input factors or parameter values (see Chapter 5). This exercise is relatively easy when the model contains a few parameters, but can become cumbersome for complex, process-based models. It is beyond the scope of this paper to review all the different methods that have been used, but one of the best examples of sensitivity analysis for process-based models may be found in Komarov et al. (2003), who carried out the sensitivity analyses for EFIMOD 2. These authors showed that the tree sub-model is highly sensitive to changes in the reallocation of the biomass increment and tree mortality functions while the soil sub-model is sensitive to the proportion and mineralisation rate of stable humus in the mineral soil. The model is very sensitive to all N compartments, including the N required for tree growth, N withdrawal from senescent needles, and soil N and N deposition from the atmosphere. For example, the prediction of stem biomass is sensitive to the N concentration in needles after abscission (Figure 18.4), reflecting the degree to which the plant (tree) controls growth by retention and internal N reallocation (Nambiar and Fife, 1991). However, although

uncertainty surrounds initial stand density (often unknown), modelled soil C and N and tree stem C (major source of carbon input to the soil sub-model) are not very sensitive to initial stand density (Figure A.5).

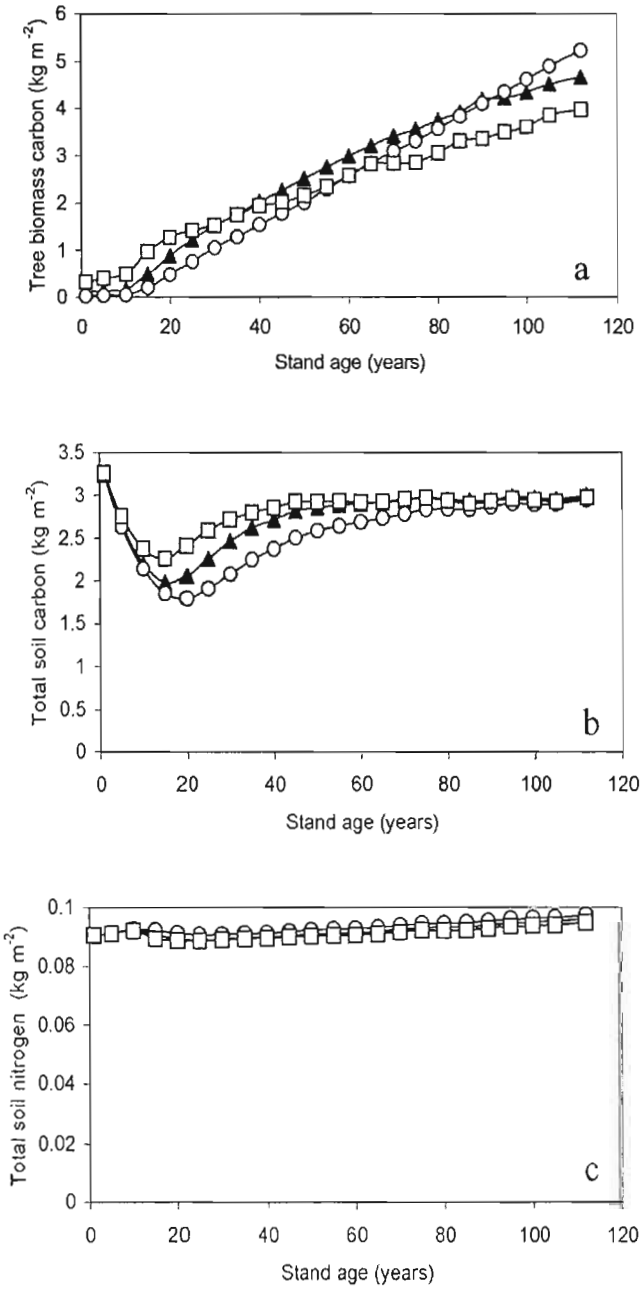

Figure A.5 Sensitivity of simulated (a) tree biomass carbon, (b) total soil carbon and (c) total soil nitrogen by EFIMOD 2 to initial stand density.

This type of uncertainty associated with sensitivity analysis could be addressed more thoroughly in the future by including Monte Carlo simulations and their variants. Very few examples of this type of integration for carbon cycle models exist (e.g. Roxburgh and Davies, 2006). One of the likely reasons is the computer time required. However, the evolution in computer technology is such that this might not be a major issue in a few years.

A.5. Conclusions

Many approaches have been developed and used to calibrate and validate process-based models. Models of the C and N cycles are generally based on sound mathematical representations of the processes involved. However, as previously mentioned, the majority of these models are deterministic. As a consequence, they do not represent adequately the error that may arise from different sources of variation. This is important, as both the C and N cycles (and models thereof) contain many sources of variation. Much can be gained by improving and standardising the use of calibration and validation methodologies both for scientists involved in the modelling of these cycles and forest managers who utilise the results.

Upscaling C dynamics from sites to regions is complex and challenging. It requires the characterisation of the heterogeneities of critical variables in space and time at scales that are appropriate to the ecosystem models, and the incorporation of these heterogeneities into field measurements or ecosystem models to estimate the spatial and temporal change of C stocks and fluxes. The success of upscaling depends on a wide range of factors, including the robustness of the ecosystem models across the heterogeneities, necessary supporting spatial databases or relationships that define the frequency and joint frequency distributions of critical variables, and the right techniques that incorporate these heterogeneities into upscaling processes. Natural and

human disturbances of landscape processes (e.g. fires, diseases, droughts and deforestation), climate change, as well as management practices, will play an increasing role in defining carbon dynamics at local to global scales. Therefore, methods must be developed to characterise how these processes change in time and space.

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APPENDIX 2

Meta-analysis and its application in global change research

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B.1. ABSTRACT

Meta-analysis is a quantitative synthetic research method that statistically integrates results from individual studies to find common trends and differences. With increasing concern over global change, meta-analysis has been rapidly adopted in global change research. Here, we introduce the methodologies, advantages and disadvantages of meta-analysis, and review its application in global climate change research, including the responses of ecosystems to global warming and rising CO_2 and O_3 concentrations, the effects of land use and management on climate change and the effects of disturbances on biogeochemistry cycles of ecosystem. Despite limitation and potential misapplication, meta-analysis has been demonstrated to be a much better tool than traditional narrative review in synthesizing results from multiple studies. Several methodological developments for research synthesis have not yet been widely used in global climate change researches such as cumulative meta-analysis and sensitivity analysis. It is necessary to update the results of meta-analysis on a given topic at regular intervals by including newly published studies. Emphasis should be put on multi-factor interaction and long-term experiments. There is great potential to apply meta-analysis to global climate change research in China because research and observation networks have been established (e.g. ChinaFlux and CERN), which create the need for combining these data and results to provide support for governments' decision making on climate change. It is expected that meta-analysis will be widely adopted in future climate change research.

Keywords: meta-analysis, global climate change

B.2. INTRODUCTION

Climate change has been one of the greatest challenges to sustainable development. Global average temperature has increased by approximately 0.6°C over the past 100 years and is projected to continue to rise at a rapid rate; global atmospheric carbon dioxide (CO_2) concentration has risen by nearly 38% since the pre-industrial period and will surpass 700 umol/mol by the end of this century [1]. Most of the warming over the last 50 years is attributable to human activities, and human influences are expected to continue to change atmospheric composition throughout the 21st century. Climate change has the potential to alter ecosystem structure (plant height and species composition) and functions (photosynthesis and respiration, carbon assimilation and biogeochemistry cycle). The change in ecosystem is expected to alter global climate through feedback mechanisms, which will have effects on human activities and these feedback mechanisms as well. Therefore, climate change, human influences and ecosystem response have become more and more interconnected. However, these direct and indirect effects on ecosystems and climate change are likely to be complex and highly vary in time and space [2]. Results from many individual studies showed considerable variation in response to climate change and human activities. Given the scope and variability of these trends, global patterns may be much more important than individual studies when assessing the effects of global change [3, 4]. There is a clear need to quantitatively synthesize existing results on ecosystems and their responses to global change and land use management in order to either reach the general consensus or summarize the difference. Meta-analysis refers to a technique to statistically synthesize individual studies [5], which has now become a useful research method [6] in global change research.

Since Gene Glass [7] invented the term "meta-analysis", it has been widely applied and developed in the fields of psychology, sociology, education, economics and medical science. It was adapted in ecology and evolutionary biology at the beginning of the 1990s [8]. Earlier introduction and review of the use of meta-analysis in ecology and evolutionary biology were given by Gurevitch et al. [9] and Arnqvist et al. [10]. In

1999, a special issue on meta-analysis application in ecology was published in Ecology, which systematically discussed case studies, development and problems on its use in ecology [11]. In China, meta-analysis has been widely applied in medical science since Zhao et al. [12] firstly introduced metaanalysis into this field. It was mainly used to synthesize the data on control and treatment experiments to determine average effect and magnitude of treatments effects and find the variance among individual studies. Peng et al. [13] were the first to introduce meta-analysis into ecology in China and provided a review on its application in ecology and medical science [14] in recent years.

Meta-analysis has been increasingly applied in largescale global change ecology in recent years and shows high value on studying some popular research issues related with global change such as the response of terrestrial ecosystem to elevated CO_2 and global warming. Unfortunately, there are very few reports available on the use of meta-analysis to examine global climate change in China [15, 16]. This paper reviews the general methodology of meta-analysis, assesses its advantages and disadvantages, synthesizes its use in global climate change and discusses future direction and potential application.

B.3. Meta-analysis method

B.3.1 Principles and steps

Researches very rarely generate identical answers to the same questions. It is necessary to synthesize the results from multiple studies to reach a general conclusion and find the difference and further direction. Meta-analysis is such a method. The term "meta-analysis" was coined in 1976 by the psychologist Glass [7] who defined it as the statistical analysis of a large collection of analytical results for the purpose of integrating the findings. It is considered as a quantitative statistical method to synthesize multiple independent studies with related hypothesis. "Meta" is from the Greek for "after". Meta-analysis was translated into different Chinese terms in different fields. Traditionally, reviewing has been done by narrative reviews, where

results are easily affected by subjective decision and preference. Meta-analysis allows one to quantitatively combine the results from individual studies to draw general conclusions and find their differences and the corresponding reasons. It is also called "analysis of analysis".

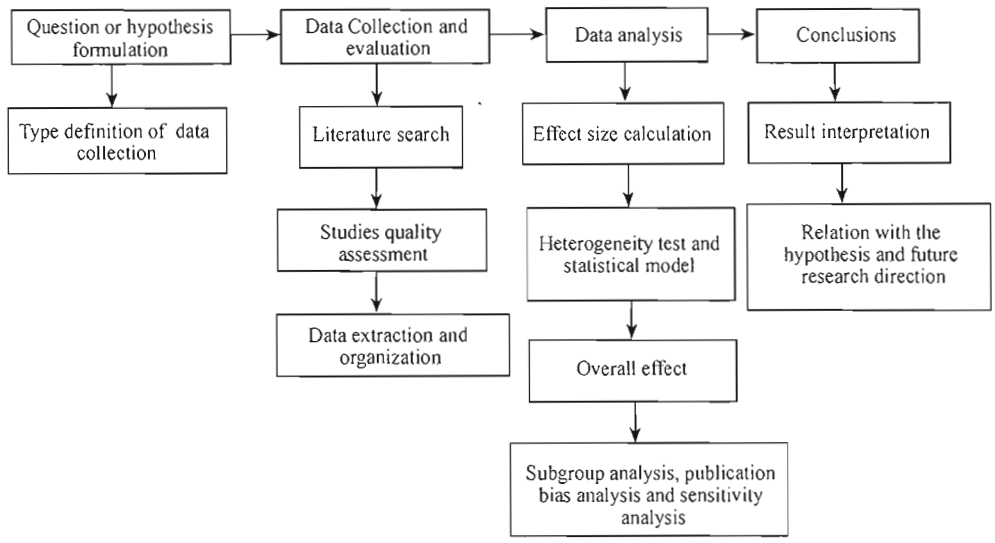

Figure B.1 Steps for performing meta-analysis.

The steps of performing meta-analysis follow the framework of scientific research: formulating research question, collecting and evaluating data analyzing the data, and interpreting the results. Figure B.1 presents the systematic review process [5, 6, 17]: (i) Research question or hypothesis formulation. For example, how does temperature increase affect tree growth? (ii) Collection of data from individual studies related to the problem or hypothesis. It is desirable to include all of relevant researches (journals, conference proceedings, thesis and reports, etc.). Criteria for inclusion of studies in the review and assessment of studies quality should be explicitly documented. (iii) Data organization and classification. Special forms for recording information extracted from selected literatures should be designed, which include basic study methods, study design, measurement results and publication sources, etc. (iv) Selection of effect size

metrics and analysis models. Effect size is essential to meta-analysis. We use the effect size to average and standardize results from individual studies. It quantifies the magnitude of standardized difference between a treatment and control condition. An appropriate effect size measure should be chosen according to the data available from the primary studies and their meanings [5, 8, 17]. Heterogeneity test should be done to determine the consistence of the results across studies.

Statistical models (fixed-effects models, random-effects models and mixed effects models) can also be used. (v) Conduct of summary analyses and interpretation. Individual effect sizes are averaged in a weighted way. Therefore, total average effect and its confidential interval are produced and showed directly as a forest plot (Figure B.2) to determine whether there is evidence for the hypothesis. The source of heterogeneity and its impacts on averaged effect size should be discussed. If some factors had great influences on the effect size, quantitative pooling would be conducted separately for each subgroup of the studies. Diagnosis and control of publication bias and sensitive analysis should be also performed.

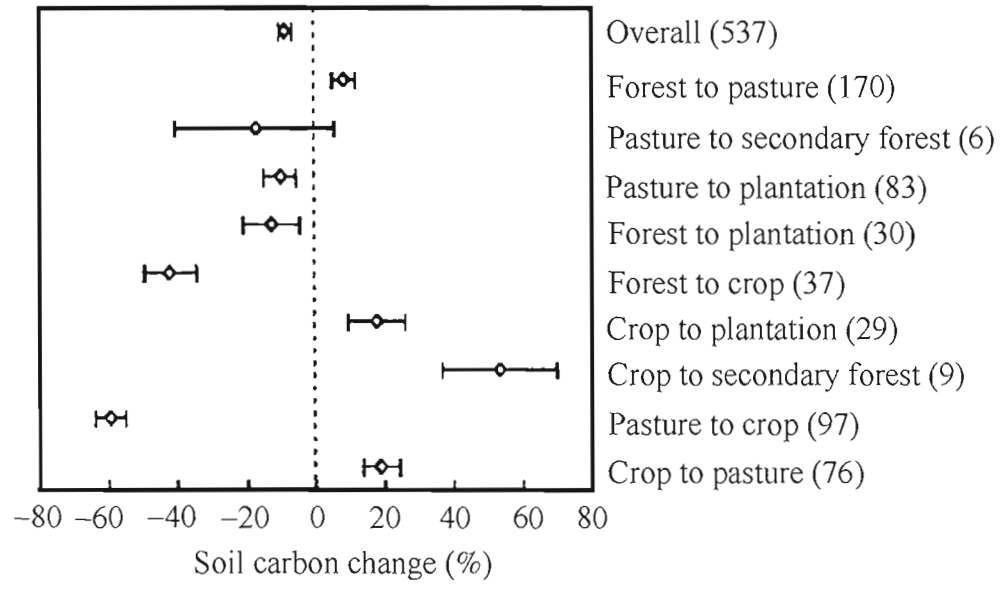

Figure B.2 Effect sizes and their confidential intervals of the effect of land use changes on soil carbon [18].

B.3.2 Advantages and disadvantages

As a new method, exact procedure and methodologies of meta-analysis are being developed [9, 19, 20]. While traditional reviewing done by the narrative reviews can provide useful summaries of the knowledge in a discipline that can be largely subjective, it may not give quantitative synthesis information. It is difficult to answer some complex questions, such as how large is the overall effect? Is it significant? What is the reason attributable to the inconsistence of the results from individual studies [8]? However, meta-analysis provides a means of quantitatively integrating results to produce the average effect; it improves the statistical ability to test hypotheses by pooling a number of datasets [17, 21]. It can be used to develop general conclusions, delimit the differences among multiple studies and the gap in previous studies, and provide the new research directions and insights. Criticisms of meta-analysis are due to its shortcomings and misapplications [17, 21], including publication bias, subjectivity in literature selection and non-independence among studies. Publication bias is defined as bias due to the influence of research findings on submission, review and editorial decisions, and may arise from bias at any of the three phases of the publication process [22, 23]. For example, studies with significant treatment effects results tend to be published more easily than those without treatment effects. Various methods are developed to verify the publication bias [24—28]. When bias is detected, further analysis and interpretation should only be carried out with caution [19].

B.3.3 Special software

Many software packages for performing meta-analysis have been developed (http://www.um.es/facpsi/metaanalysis/software.php), some of which are listed in Table 1. Besides special meta-analysis software, general statistical software packages such as SAS and STAT also have standard meta-analysis functions. These programs differ in the data input format, the measures of effect sizes, statistical models, figures drawing and whether some functions such as cumulative meta-analysis and sensitive analysis should be included. Of all the mentioned software, CMA, MetaWin, RevMan and WeasyMA have user-friendly interfaces and powerful functions covering

calculation of effect sizes, fixed-effect and random-effect models, heterogeneity test, subgroup analysis, publication bias analysis, cumulative meta-analysis and meta-regression. MetaWin provides non-parameter tests and statistic conversions. CMA gives the function for sensitivity analysis. After conducting online literature search for which meta-analysis software packages were most commonly used in published journal papers from Elsevier, Springer and Blackwell publishers, we found that the most frequently used packages are RevMan (270 papers), MetaWin (80 papers) and DSTAT (60 papers).

Table 1 Software for meta-analysis

Software	Website	Description
Comprehensive meta-analysis (CMA)	http://www.meta-analysis.com/	commercial software/Windows
MetaWin	http://www.metawinsoft.com	commercial software/Windows
DSTAT	http://www.erlbaum.com	commercial software/Dos
WeasyMA	http://www.weasyma.com/	commercial software/Windows
Review Manager (RevMan)	http://www.cc-ims.net/RevMan/	free software/Windows
Meta-DiSc	http://www.hrc.es/investigacion/metadisc_en.htm	free software/Windows
Meta	http://userpage.fu-berlin.de/~health/meta_e.htm	free software/Dos
EasyMA	http://www.spc.univ-lyon1.fr/easyma.dos/	free software/Dos
MetaTest	http://www.medepi.net/meta/MetaTest.html	free software/Dos
Meta calculator	http://www.lyonsmorris.com/lyons/metaAnalysis/index.cfm	free online calculation
SAS/S-plus/STAT/SPSS	http://www.sas.com, http://www.insightful.com/, http://www.stata.com, http://www.spss.com	general statistical software with meta-analysis function

B.4 Case studies of meta-analysis in global climate changes

Since the first research on meta-analysis conducted in global climate change [29], meta-analysis has been increasingly utilized in this field. Figure 3 presents the number of publications from 1996 to 2005 that used meta-analysis for global climate change research. It shows an increasing trend in general.

B.4.1 Response of ecosystem to elevated CO_2

It is recognized that CO_2 concentration in the atmosphere and global temperature are increasing. CO_2 is not only one of the main gases responsible for the greenhouse effect,

but an essential component for photosynthesis, plant growth and ecosystem productivity as well. Increasing CO_2 concentration results in rising temperature, which alters carbon cycle of terrestrial ecosystem. Response of ecosystem to elevated CO_2 is important to global carbon cycle [30, 31] and is an essential research issue in ecology and climate change research. Research using meta-analysis has addressed some ecological processes and relationships, including plant photosynthesis and respiration, growth and competition, productivity, leaf gas exchange and conductance, soil respiration, accumulation of soil carbon and nitrogen, the relations between light environment and growth, and photosynthesis and leaf nitrogen.

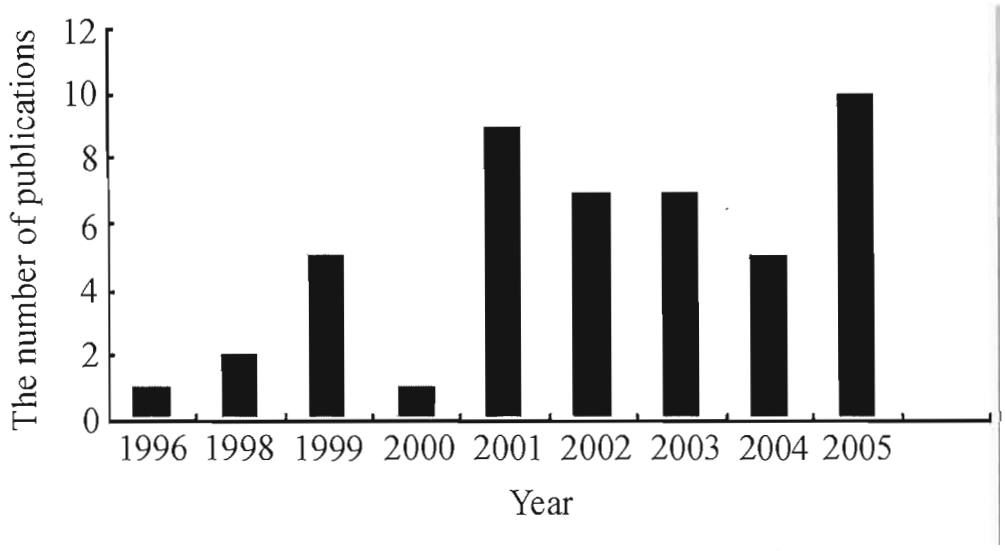

Figure B.3 The number of publications using meta-analysis for climate change research from 1996 to 2005.

The effect of elevated CO_2 on plant growth is generally positive. Curtis et al. [32] used meta-analytical methods to summarize and interpret more than 500 reports of effects of elevated CO_2 on woody plant biomass accumulation. They found total plant biomass significantly increased by 28.8% and the responses to elevated CO_2 were strongly affected by environmental stress factors and to a less degree by duration of CO_2 exposure and functional groups. In another study on the response of C3 and C4 plants to elevated CO_2, Wand et al. [33] used mixed-effect model for meta-analysis to show

that total biomass has increased by 33% and 44% in elevated CO_2 for both C3 and C4 plants, respectively. These authors also found C3 and C4 plants have different morphologi cal developments under elevated CO_2. C3 plants developed more tillers and increased slightly in leaf area. By contrast, C4 plants increased in leaf area with slight increase in tiller numbers. A significant decrease in leaf stomatal conductance, as well as increased water use efficiency and carbon assimilation rate were also detected. These results have important implications for the water balance of important catchments and rangelands, particularly in sub-tropical and temperate regions. Their study also implied that it might be premature to predict that the C4 type will lose its competitive advantage in certain regions as CO_2 levels rise, based only on different photosynthetic mechanisms. Environmental factors (soil water deficit, low soil nitrogen, high temperature and high concentration O3) significantly affected the response of plants to elevated CO_2. The total biomass has increased by 30.01% for C3 plants under unstressed condition [16]. Kerstiens [34] used meta-analysis to test the hypothesis that variation of growth responses of different tree species to elevated CO_2 was associated with the species' shade-tolerance. This study showed that in general, relatively more shade-tolerant species experienced greater stimulation of relative growth rate by elevated CO_2. Pooter et al. [35] evaluated the effects of increased atmospheric CO_2 concentrations on vegetation growth and competitive performance using meta-analysis. They detected that the biomass enhancement ratio of individually grown plants varied substantially across experiments and that both species and size variability in the experimental populations was a vital factor. Responses of fast-growing herbaceous C3 species were much stronger than those of slow-growing C3 herbs and C4 plants. CAM species and woody plants showed intermediate responses. However, these responses are different when plants are growing under competition. Therefore, biomass enhancement ratio values obtained for isolated plants cannot be used to estimate those of the same species growing in interspecific competition.

Meta-analysis was also performed to summarize a suite of photosynthesis model parameters obtained from 15 field-based elevated CO_2 experiments of European forest tree species [36]. It indicated a significant increase in photosynthesis and a down-

regulation of photosynthesis of the order of 10%—20% to elevated CO_2. There were significant differences in the response of stomata to elevated CO_2 between different functional groups (conifer and deciduous), experimental durations, and tree ages. Ainsworth et al. [37] made the first meta-analysis of 25 variables describing physiology, growth and yield of single crop species (soybean). The study supported that the rates of acclimation of photosynthesis were less in nitrogen-fixing plants and stimulation of photosynthesis of nitrogen-fixing plants was significantly higher than that of non-nitrogen-fixing plants. Pot size significantly affected these trends. Biomass allocation was not affected by elevated CO_2 when plant size and ontogeny were considered. This was consistent with previous studies. Again, pot size significantly affected carbon assimilation, which demonstrated the importance of field studies on plant response to global change. While experiments on plant response to elevated CO_2 provide the basis for improving our knowledge about the response, most of individual species in these experiments were from controlled environments or enclosure. These studies had some serious potential limitations, for example, enclosures may amplify the down-regulation of photosynthesis and production [38]. FACE (Free Air CO_2 Enrichment) experiments allow people to study the response of plants and ecosystems to elevated CO_2 under natural and fully open-air conditions. In the metaanalysis of physiology and production data in the 12 large-scale FACE experiments across four continents [39], several results from previous chamber experiments were confirmed by FACE studies. For example, light-saturated carbon uptake, diurnal carbon assimilation, growth and above-ground production increased, while specific leaf area and stomatal conductance decreased in elevated CO_2. Different results showed that trees were more responsive than herbaceous species to elevated CO_2 and grain crop yield increased far less than anticipated from prior enclosure studies. The results from this analysis may provide the most plausible estimates of how plants growing in native environments and field will respond to elevated CO_2. Long et al. [40] also reported that average light-saturated photosynthesis rate and production increased by 34% and 20% respectively in C3 species. There was little change in capacity for ribulose-1,5- bisphosphate regeneration and little or no effect on photosynthetic rate under elevated CO_2. These results differ from enclosure studies.

Meta-analysis of the response of carbon and nitrogen in plant and soil to rising atmospheric CO_2 revealed that averaged carbon pool sizes in shoot, root, and whole plant have increased by 22.4%, 31.6%, and 23.0%, respectively, and nitrogen pool sizes in shoot, root, and whole plant increased by 4.6%, 10.0%, and 10.2%, respectively [41]. The high variability in CO_2-induced changes in carbon and nitrogen pool sizes among different CO_2 facilities, ecosystem types and nitrogen treatments resulted from diverse responses of various carbon and nitrogen processes to elevated CO_2. Therefore, the mechanism between carbon and nitrogen cycles and their interaction must be considered when we predict carbon sequestration under future global change.

The response of stomata to environment conditions and controlled photosynthesis and respiration is a key determinant of plant growth and water use [42]. It is widely recognized that increased CO_2 will cause reduced stomatal conductance, although this response is variable. For example, Curtis et al. [32] reported that stomatal conductance decreased by 11%, not significantly under elevated CO_2. In the meta-analysis on data collected from 13 long-term (>1 year), field-based studies of the effects of elevated CO_2 on European tree species [43], a significant decrease of 21% in stomatal conductance was detected, but no evidence of acclimation of stomatal conductance was found. The responses of young, deciduous and water stressed trees were even stronger than in older, coniferous and nutrient stressed trees. Using the data from Curtis et al. [32], Medlyn et al. [43] found that there was no significant difference in terms of the CO_2 effect on stomatal conductance between pot-grown and freely rooted plants, but there was a difference between shortterm and long-term studies. Short-term experiments of less than one year showed no reduction in stomatal conductance; however, longer-term experiments (> 1 year) showed 23% decrease. Compared with previous studies [36], these responses under long-term experiments were much more consistent. Thus, long-term experiments are essential to the studies of the response of stomatal conductance to elevated CO_2. Other metaanalysis studies also support the

results of the reduction of leaf area and stomatal conductance under elevated CO_2 [16, 39, 40].

Leaf dark respiration is a very important component of the global carbon budget. The response of leaf dark respiration and nitrogen to elevated CO_2 was studied by meta-analysis, which demonstrates a significant decrease [29, 32]. In a meta-analytical test of elevated CO_2 effects on plant respiration [44], mass-based leaf dark respiration (Rdm) was significantly reduced by 18%, while area-based leaf dark respiration (R_{da}) marginally increased approximately 8% under elevated CO_2. There were also significant differences in the CO_2 effects on leaf dark respiration between functional groups. For example, leaf R_{da} of herbaceous species increased, but leaf Rda of woody species did not change. Their metaanalysis reported increasing carbon loss through leaf Rd under a higher CO_2 environment and a strong dependency of Rd responses to elevated CO_2 under experimental conditions.

It is critical to understand the effects of elevated CO_2 on leaf area index (LAI) [45]. However, no consistent results have been reported [46, 47]. Meta-analysis of soybean studies showed that the averaged LAI increased by 18% under elevated CO_2 [37], however, no significant increase was found in the meta-analysis of FACE experimental data [40].

The relationship between photosynthetic rate and leaf nitrogen content is an important component of photosynthesis models. Meta-analysis combining with regression is able to assess whether the relationship was more similar to species within a community than between community and vegetation types, and how elevated CO_2 affected the relationship [48]. Approximately 50% community and vegetation types had similar relationship between photosynthetic rate and leaf nitrogen content under ambient CO_2. There were also differences of CO_2 effects on the relationship between species.

Reproductive traits are the key to investigate the response of communities and ecosystems to global change. Jablonski et al. [49] conducted the first meta-analysis of

plant reproductive response to elevated CO_2. They found that across all species, CO_2 enrichment resulted in the increase of flowers, fruits, seeds, individual seed mass and total seed mass by 19%, 18%, 16%, 4% and 25%, respectively, and the decrease of seed nitrogen concentration by 14%. There were no differences between crops and wild species in terms of total mass response to elevated CO_2, but crops allocated more mass to reproduction and produced more fruits and seeds than wild species did when they grew under elevated CO_2. Seed nitrogen in legumes was not affected by elevated CO_2 concentrations, but declined significantly for most nonlegumes. These results indicated important differences in reproductive traits between individual taxa and functional groups, for example, crops were much more responsive to elevated CO_2 than wild species. The effects of variation of CO_2 on reproductive effort and the substantial decline in seed nitrogen across species and functional groups had broad implications for function of natural and agro-ecosystems in the future.

Soil carbon is an essential pool of global carbon cycle. Using meta-analysis techniques, Jastrow et al. [50] showed a 5.6% increase in soil carbon over 2—9 years, at rising atmospheric CO_2 concentrations. Luo et al. [41] also demonstrated that averaged litter and soil carbon pool sizes at elevated CO_2 were 20.6% and 5.6% higher than those at ambient CO_2. Soil respiration is a key component of terrestrial ecosystem carbon processes. Partitioning soil CO_2 efflux into autotrophic and heterotrophic components has received considerable attention, as these components use different carbon sources and have different contributions to overall soil respiration [51, 52]. The results from partitioning studies by means of a meta-analysis indicated an overall decline in the ratio of heterotrophic component to soil carbon dioxide efflux for increasing annual soil carbon dioxide efflux [53].

The ratios of boreal coniferous forests were significantly higher than those of temperate, while both temperate and tropical latifoliate forests did not differ in ratios from any other forest types. The ratio showed consistent declines with age, but no difference was detected in different age groups. Additionally, the time step by which fluxes were partitioned did not affect the ratios consistently. It may indicate that higher

carbon assimilation in the canopy did not translate into higher sequestration of carbon in ecosystems, but was simply a faster return time through plants to return to the atmosphere via the roots.

Barnard et al. [54] estimated the magnitude of response of soil N_2O emissions, nitrifying enzyme activity (NEA), and denitrifying enzyme activity (DEA) to elevated CO_2. They found no significant overall effect of elevated CO_2 on N_2O fluxes but a significant decrease of DEA and NEA under elevated CO_2. Gross nitrification was not altered by elevated CO_2, but net nitrification did increase. Changes in plant tissue chemistry may have important and long-term ecosystem consequences. Impacts of elevated CO_2 on the chemistry of leaf litter and decomposition of plant tissues were also summarized using metaanalysis [55]. The results suggested that the nitrogen concentration in leaf litter was 7.1% lower under elevated CO2 compared with that at ambient CO_2. They also concluded that any changes in decomposition rates resulting from exposure of plants to elevated CO_2 were small when compared with other potential impacts of elevated CO_2 on carbon and nitrogen cycling. Knorr et al. [56] conducted a meta-analysis to examine the effects of nitrogen enrichment on litter decomposition and found no significant effects across all studies. However, fertilizer rate, site-specific nitrogen deposition level and litter mass have influenced the litter decay response to nitrogenaddition.

Meta-analysis was also used for investigating the responses of mycorrhizal richness [57], ectomycorrhizal and arbuscular mycorrhizal fungi, and ectomycorrhizal and arbuscular mycorrhizal plants [58] to elevated CO_2.

B.4.2 Response of ecosystem to global warming

The potential effects of global warming on environment and human life are numerous and variable. Increasing temperature is expected to have a noticeable impact on terrestrial ecosystems. Data collected from 13 different International Tundra Experiment (ITEX) sites [59] were used to analyze responses of plant phenology, growth and reproduction to experimental warming using meta-analysis. This analysis

suggests that the primary forces driving the response of ecosystems to soil warming do vary across climatic zones, functional groups and through time. For example, herbaceous plants had stronger and more consistent vegetative and reproductive response than woody plants. Recently, similar work was done by Walker et al. [60] who used meta-analysis to test plant community response to standardized warming experiments at 11 locations across the tundra biome involved in ITEX after two growing seasons. They revealed that height and cover of deciduous shrubs and graminoids have increased, but, cover of mosses and lichens has decreased, and species diversity and evenness have decreased under the warming. Graminoids and shrubs showed larger changes over 6 years. This was somewhat different from previous study [59] in which graminoids and shrubs had the largest initial growth over 4 years. This again demonstrates that longer-term experiments are essential for investigating plant response to global warming. Parmesan et al. [3] reported a metaanalysis on species range-boundary changes and phenological shifts to global warming, which showed significant range shifts averaging 6.1 km per decade towards the poles and significant mean advancement of spring events by 2.3 days per decade. Similar results were found in another study on the effects of global warming on plant and animals [61]. More than 80 percent of species showed changes associated with temperature. Species at higher latitudes responded more strongly to the more intense change in temperature. A statistically significant change towards earlier timing of spring events has also been detected. The sensitivity of soil carbon to temperature plays an important role in the global carbon cycle and is particularly important for giving the potential feedback to climate change [62]. However, the sensitivity of soil carbon to warming is a major uncertainty in projections of CO_2 concentration and climate [56]. Recently, the sensitivity of soil respiration and soil organic matter decomposition has received great attention [56, 62—68]. Several experiments showed that soil organic carbon decomposition increased with higher temperatures [63, 68], but additional studies gave contrary results [64—66]. Although results from individual studies showed great variation in response to warming, results from the meta-analysis showed that 2—9 years of experimental warming at 0.3—6.0℃ significantly increased soil respiration rates by 20% and net nitrogen mineralization rates by 46% [2]. The magnitude of the

response of soil respiration and nitrogen mineralization rates to experimental warming was not significantly related to geographic, climatic, or environmental variables. There was a trend toward decreasing response to soil temperature as the study duration increased. This study implies the need to understand the relative importance of specific factors (such as temperature, moisture, site quality, vegetation type, successional status and land-use history) at different spatial and temporal scales. Barnard et al. [54] showed that the effects of elevated temperature on DEA, NEA, and net nitrification were not significant. Based on the meta-analysis results of plant response to climate change experiments in the Arctic [69], elevated temperature significantly increased reproductive and physiological measures, possibly giving positive feedbacks to plant biomass. The driving force of future change in arctic vegetation was likely to increase nutrient availability, arising for example from temperature-induced increases in mineralization. Arctic plant species differ widely in their responses to environmental manipulations. Shrub and herb showed strongest response to the increase of temperature. The study advocated a new approach to classify plant functional types according to species responses to environmental manipulations for generalization of responses and predictions of effects. Raich et al. [70] applied metaanalyses to evaluate the effects of temperature on carbon fluxes and storages in mature moist tropical evergreen forest ecosystems. They found that litter production, tree growth and belowground carbon allocation all increased significantly with the increasing site mean annual temperature; but temperature had no noticeable effect on the turnover rate of aboveground forest biomass. Soil organic matter accumulation decreased with the increasing site mean annual temperature, which indicated that decomposition rates of soil organic matter increased with mean annual temperature faster than rates of NPP. These results imply that in a warmer climate, conservation of forest biomass will be critical to the maintenance of carbon stocks in moist tropical forests. Blenckner et al. [71] tested the impact of the North Atlantic Oscillation (NAO) on the timing of life history events, biomass of organisms and different trophic levels. They found that the response of life history events to the NAO was similar and strongly affected by NAO in all environments including freshwater, marine, and terrestrial ecosystems. The early timing of life history events was detected owing to warming winter, but less

pronounced at high altitudes. The magnitude of response of biomass was significantly associated with NAO, with negative and positive correlations for terrestrial and aquatic ecosystems, respectively.

Few case studies using meta-analysis have explored the combined effects of elevated CO_2 concentrations and temperature on ecosystem. One possible reason may be due to the lack of individual studies examining both factors simultaneously. Zvereva et al. [72] performed meta-analysis to evaluate the consequences of simultaneous elevation of CO_2 and temperature for plant-herbivore interactions. Their results showed that nitrogen concentration and C/N ratio in plants decreased under simultaneous increase of CO_2 and temperature, whereas elevated temperature had no significant effect on them. Insect herbivore performance was adversely affected by elevated temperature, favored by elevated CO_2, and not modified by simultaneous increase of CO_2 and temperature. Their analysis distinguished three types of relationships between CO_2 and elevated temperature: (i) the responses to elevated CO_2 are mitigated by elevated temperature (nitrogen, C/N, leaf toughness), (ii) the responses to elevated CO_2 do not depend on temperature (sugars and starch, terpenes in needles of gymnosperms, insect performance) and (iii) these effects emerge only under simultaneous increase of CO_2 and temperature (nitrogen in gymnosperms, and phenolics and terpenes in woody tissues). The predicted negative effects of elevated CO_2 on herbivores are likely to be mitigated by temperature increase. Therefore, the conclusion is that elevated CO_2 studies cannot be directly extrapolated to a more realistic climate change scenario.

B.4.3 Response of ecosystem to O_3

Mean surface ozone concentration is predicted to increase by 23% by 2050 [1]. The increase may result in substantial losses of production and reproductive output. Individual studies on the response of vegetation to ozone varied widely because ozone effects are influenced by exposure dynamics, nutrient and moisture conditions, and the species and cultivars. In the meta-analysis on the response of soybean to elevated ozone [73] from chamber experiments, the average shoot biomass was decreased by about 34% and seed yield was about 24% lower than that without ozone at maturity.

The photosynthetic rates of the topmost leaves were decreased by 20%. Searles et al. [74] provided the first quantitative estimates of UV-B effects in field-based studies on vascular plants using meta-analysis. They detected that several morphological parameters such as plant height and leaf mass per area showed little or no response to enhanced UV-B, and leaf photosynthetic processes and the concentration of photosynthetic pigments were also not affected. But shoot biomass and leaf area presented modest decreases under UV-B enhancement.

B.4.4 The effects of land use change and land management on climate change

Land use change and land management are believed to have an impact on the source and sink of CO_2, CH_4 and N_2O. Guo et al.[18] examined the influence of land use changes on soil carbon stocks based on 74 publications using the meta-analysis. Their analysis indicated that soil carbon stocks declined by 10% after land use changed from pasture to plantation, e.g. 13% decrease for converting native forest to plantation, 42% for converting native forest to crop, and 59% for converting pasture to crop. Soil carbon stocks can increase by 8% after land use changed from native forest to pasture, 19% from crop to pasture, 18% from crop to plantation, and 53% from crop to secondary forest, respectively. Ogle et al. [75] quantified the impact of changes of agricultural land use on soil organic carbon storage under moist and dry climatic conditions in temperate and tropical regions using meta-analysis and found that management impacts were sensitive to climate in the following order from largest to smallest in terms of changes in soil organic carbon: tropical moist > tropical dry > temperate moist > temperate dry. Their results indicated that agricultural management impacts on soil organic carbon storage varied depending on climatic conditions influencing the plant and soil processes driving soil organic matter dynamics. Zinn et al. [76] studied the magnitude and trend of effects of agriculture land use on soil organic carbon and showed that intensive agriculture systems caused significant soil organic carbon loss of 10.3% at the 0—20 cm depth, while nonintensive agriculture systems had no significant effect on soil organic carbon stocks at the 0—20 and 0—40 cm depths, however, in coarse-textured soils, non-intensive agriculture systems caused significant soil organic carbon losses of about 20% at 0—20 and 0—40 cm depths.

It is important to understand the effects of forest management on soil carbon and nitrogen because of their roles in determining soil fertility and a source or sink of carbon at a global scale. Johnson et al. [77] reviewed various studies and conducted a meta-analysis on forest management effects on soil carbon and nitrogen. They found that forest harvesting generally had little or no effect on soil carbon and nitrogen. However, there were significant effects of harvest types and species on them. For example, sawlog harvesting can increase by about 18% of soil carbon and nitrogen, while whole tree harvesting may cause 6% decrease of soil carbon and nitrogen. Both fertilization and nitrogenfixing vegetation have caused noticeable overall increases in soil carbon and nitrogen. Meta-regression was used to examine the costs and carbon accumulation for switching from conventional tillage to no-till, and the costs of creating carbon offset by forestry [78, 79]. The results showed that the viability of agricultural carbon sinks varied with different regions and crops. The increase of soil carbon resulting from no-till system may change with the types of crops, region, measured soil depth and the length of time at which no-till was practised. Another meta-analysis on the driver of deforestation in tropical forests demonstrated that deforestation was a complex and multiform process and better understanding of these complex interactions would be a prerequisite to perform realistic projections of land-cover changes based on simulation models [80].

B.4.5 Effects of disturbances on biogeochemistry

Wan et al.[81] examined the effects of fire on nitrogen pool and dynamics in terrestrial ecosystems. They found that fire significantly decreased fuel N amount by 58%, increased soil NH_4+ by 94% and NO_3- by 152%, but had no significant influences on fuel N concentration, soil N amount and concentration. The results suggested that different ecosystems had different mechanisms and abilities to replenish nitrogen after fire, and fire management regimes (including frequency, interval, and season) should be determined according to the ability of different ecosystems to replenish nitrogen. Fire had no significant effects on soil carbon or nitrogen, but duration after fire had a significant effect, with an increase in both soil carbon and N after 10 years [77].

However, there were significant differences among treatments, with the counterintuitive result of lower soil carbon following prescribed fire and higher soil carbon following wildfire.

B.5 Discussion

Meta-analysis has been widely applied in global climate change research and proved a valuable tool in this field. Particularly, the response of terrestrial ecosystem to elevated CO_2, global warming and human activities received considerable interests because of its importance in global climate change and numerous existing individual and ongoing studies. In general, meta-analysis can statistically draw more general and quantitative conclusions on some controversial issues compared with single studies, identify the difference and its reasons, and provide some new insights and research directions.

B.5.1 Some issues

(i) Some basic issues on meta-analysis still exist [8,11,14,23,82], including publication bias, the choice of effect size measures, the difficulty of data loss when selecting literatures, quality assessment on literatures and non-independence among individual studies. There are a lot of discussions on publication bias because it can directly affect the conclusions of meta-analysis. Recently, a monograph was published, relating the types of publication bias, possible mechanisms, existing empirical proofs, statistical methods to describe it and how to avoid it [28]. Methods detecting and correcting publication bias included proportion of significant studies, funnel graphs and some statistical methods (fail-safe number, weighted distribution theory, truncated sampling and rank correlation test, etc.)[83]. We found that the natural logarithm of response ratio was the most frequently used measure in global change research. The advantage is that it can linearize the response ratio, being less sensitive to changes in a small control group, and provide a more normal sampling distribution for small samples [4, 84]. In addition, the conclusions derived from meta-analysis depend on the quantity and quality of single studies. Many studies do not adequately report sample size and variance, which made weighted effect analysis difficult. Therefore, publication quality

needs to be assessed through making strict literature selection and selecting quality evaluation indicators. However, publication bias and data loss are also shared with traditional narrative reviews. It is necessary for authors to report their experiments in more detail to improve publication quality and for editors to publish all high-qualified studies without considering the results. All these could improve the quality of meta-analysis in the future.

(ii) There are also risks of misusing meta-analysis, so we must be very cautious to analyze the results. Körner [85] expressed doubt in the meta-analysis on CO_2 effects on plant reproduction [49], in which a surprising conclusion was that the interacting environmental stress factors are not important drivers of CO_2 effects on plant reproduction. Körner [85] thought that the meta-analysis provided rather limited insight because the data were not stratified by fertility of growing conditions and the resource status of test plants was not known. The authors advised that meta-analysis on aspects of CO_2 impact research must account for the resource status of test plants, and that plant age is a key criterion for grouping. They also emphasized the shift in data treatment from technology-oriented or taxonomy-oriented criteria to that control sink activity of plants, i.e. nutrition, moisture, and developmental stage. In a re-analysis [86] of meta-analysis on the stress-gradient hypothesis [87], it is revealed that many studies used by Maestre et al. [87] were not conducted along stress gradients and the number of studies was not enough to differ the points on gradients among studies. Therefore, the re-analysis did not support their original conclusions under more rigorous data selection criteria and changing gradient lengths between studies and covariance.

(iii) Some advanced methods for meta-analysis have not been applied in global climate change research. Gates [88] pointed out that many methods used for reducing bias and enhancing the accuracy, reliability and usefulness of reviews in medical science have not yet been widely used by ecologists. In global climate change research, cumulative meta-analysis, meta-regression and sensitivity analyses, for example, have not been applied and reported. Cumulative meta-analysis is a series of meta-analyses in which

studies are added to the analysis based on a predetermined order to detect the temporal trends of effect size changes and test possible publication bias [89]. It is useful to update summary results from meta-analysis. The temporal changes of the magnitude of effect sizes were found to be a general phenomenon in ecology [90]. Meta-regression can quantitatively reflect the effects of data, methods and related continuous variables on effect sizes and be used for prediction. Sensitive analysis was proposed to examine the robustness of conclusions from meta-analysis because of the subjective factors. It tests the changes of the conclusions after changing data treatments or models, for example, re-analysis after removing low-quality studies, stratified meta-analysis according to sample sizes and re-analysis after changing selected and removed literature criteria [91]. These methods still have potential to be used in global climate change research.

(iv) It is necessary to update the results of metaanalysis for a given topic at regular intervals. The accumulation of science evidence is a dynamic process, which cannot be satisfactorily described by the mean effect size from meta-analysis alone at a single time point. Meta-analyses of studies on the same topic performed at different time points may lead to different conclusions. Therefore, it is important to update the results of meta-analysis for a given topic at regular intervals by including newly published studies.

(v) More emphases should be put on the effects of multi-factor interactions and long-term experiments in global climate change research. The impact of climate change is related to various fields including population genetics, ecophysiology, bioclimatology, plant geography, palaeobiology, modeling, sociology, economics, etc. Meta-analysis has not been adopted in some fields or topics such as the impact of climate change on forest insect and disease occurrence, modeling the response of ecosystem productivity to climate change, and the impact of climate change on some ecosystem as a whole. In addition, few studies were conducted on multi-factor interaction although the interaction exists in climate change in the real world [31]. For example, soil respiration is regulated by multiple factors, including temperature, moisture, soil pH, soil depth

and plant growth condition. Those factors and their interaction have complicated effects on soil respiration. In FACE experiments, although elevated CO_2 alone increased NPP, the interactive effects of elevated CO_2 with temperature, N, and precipitation on NPP were less than those of ambient CO_2 with those factors [92]. These results clearly indicated the need for multi-factor experiments. The impact of climate change over time is also an important issue. Particularly, most experiments on trees have been conducted for a very short term. The longest FACE experiment for forest has been established only for 10 years up to now (http://c-h2oecology.env.duke.edu/site/face.html). Long-term experiments are still needed.

B.5.2 Potential application of meta-analysis in climate change research in China

Changes of global pattern are much more important than single case study in global climate change research. Therefore, meta-analysis has great potential to be used in this field. Although meta-analysis has some limitations and risks, it has been proved to be a valuable statistical technique synthesizing multiple studies. It provides a tool to view the larger trends, thus can answer the question on larger temporal and spatial scales that single experiment cannot do. China, with its diverse vegetations and land uses, has complicated climate regions across tropical, sub-tropical, warm temperate, temperate and cold zones from south to north and plays an important role in global climate change. In addition, China has the potential to affect climate change because of its gas emission development after Tokyo Protocol came into effect. It faces a great pressure and challenge and needs scientifically sound decisions on climate change issue. Scientists have made progress and conducted many experiments and accumulated large amount of original data and results. For example, Chinese Terrestrial Ecosystem Flux Observational Research Network (ChinaFLUX) consists of 8 micrometeorological 300 method-based observation sites and 17 chamber method-based observation sites (http://www.chinaflux.org). It measures the output of CO_2, CH4 and N_2O for 10 main terrestrial ecosystems in China. Chinese Ecosystem Research Network (CERN) is composed of 36 field research stations for various ecosystems, including agriculture, forestry, grassland, desert and water body (http://www.cern.ac.cn). It is necessary and important to synthesize these large amounts of data and results in order to answer some

overall scientific questions at larger scale, so that the results from meta-analysis could provide scientific information and evidence for governmental decisions on climate change. It is believed that the future of meta-analysis is promising with wide application in global climate change research.

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APPENDIX 3

Application of meta-analysis in quantifying the effects of soil warming on soil respiration in forest ecosystems

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C.1. ABSTRACT

No consensus has emerged on the sensitivity of soil respiration to increasing temperatures under global warming due partly to the lack of data and unclear feedbacks. Our objective was to investigate the general trends of warming effects on soil respiration. This study used meta-analysis as a means to synthesize data from eight sites with a total of 140 measurements taken from published studies. The results presented here suggest that average soil respiration in forest ecosystems was increased approximately by 22.5% with escalating soil temperatures while soil moisture was decreased by 16.5%. The decline in soil moisture seemed to be offset by the positive effects of increasing temperatures on soil respiration. Therefore, global warming will tend to increase the release of carbon normally stored within forest soils into the atmosphere due to increased respiration.

KEY WORDS: Forest ecosystem, meta-analysis, soil respiration, soil warming

C.2.INTRODUCTION

Soil respiration plays a major role in the global carbon cycle, being influenced by both biotic factors, like human activities, and abiotic factors, like substrate supply, temperature, and moisture (Ryan and Law, 2005; Trumbore, 2006). All of these factors are also interrelated and interact with each other. Temperature and moisture are key factors that regulate many terrestrial biological processes, including soil respiration (Raich and Potter, 1995). It is mainly accepted that anthropogenic activities have caused the escalating atmospheric CO_2 concentrations and increased temperatures seen today (IPCC, 2007). However, recent evidence concerning the impact of global warming on soil respiration is inconsistent. For instance, several results based on gradient observations and incubation experiments indicate that the decomposition of soil organic matter (SOM) did not vary with temperature (Liski *et al.,* 1999; Giardina and Ryan, 2000). On the other hand, study results from Trumbore *et al.* (1996), Agren and Bosatta (2002) and Knorr *et al.* (2005) suggest that soil carbon turnover rates increase with temperature. These inconsistencies may be caused by spatial and temporal variations in environmental conditions. Likewise, soil moisture may decrease due to an increase in temperature (Wan *et al.,* 2002). It is important to note, however, that influences of moisture reduction on soil respiration are poorly understood (Raich and Potter, 1995; Davidson *et al.,* 1998; Fang and Moncrieff, 1999; Xu *et al.*, 2004).

To better understand global warming effects on carbon exchange between the terrestrial biosphere and the atmosphere, broader scale studies (e.g., at continental and global scale) are essential. However, results from large individual studies have shown considerable variation in response to warming. Despite these research efforts, no consensus has emerged concerning the sensitivity of temperature on soil respiration. A better understanding can be attained by quantitatively synthesizing existing data on ecosystem respiration and its potential response to global warming. Meta-analysis is a technique developed specifically for the statistical synthesis of independent experiments (Hedges and Olkin, 1985; Gurevitch et al., 2001) and has been used recently for global warming impacts studies (Parmesan et al., 2003; Luo et al., 2006;

Morgan et al., 2006). Rustad et al. (2001) conducted a meta-analysis to summarize the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming across 32 sites around the world utilizing different biome types (forest, grassland and tundra). They also concluded that soil respiration would generally increase by 20% if experimental warming was within the range of 0.3 to 6.0°C, and a down-regulation would take place within 1 to 5 years. However, their study did not separate forests from other biomes, and only provided an overall effect. It is therefore important to continuously integrate new warming research results using meta-analysis to further understand the effects of temperature on soil respiration.

The objectives of this study are thus to: (1) use meta-analysis to quantitatively examine whether increased temperature stimulates soil respiration and decreases soil moisture in forest ecosystems; (2) estimate the magnitude of the effects of temperature on soil respiration and soil moisture.

C.3.MATERIAL AND METHODS

C.3.1 Data collection

In this study, eight sites with a total of 140 measurements collected from soil warming experiments in the field were compiled from published papers (see Table 1). Only soil warming experiments were selected in order to isolate warming effects from other environmental factors. The data selection criterion was as follows: in both the control and heated plots, the mean and standard deviation values had to be provided. If data were presented graphically, authors were contacted for verification or values were estimated from digitized figures manually. Data covers several vegetation types including mixed deciduous forest, mixed coniferous forest as well as Douglas fir and Norway spruce forest stands distributed within eight different sites. An approximate 4.8°C mean increase in soil temperature was established across all eight study sites, with a range from 2.5 to 7.5°C. The study periods lasted from one to ten years.

Table 1. Basic site-specific information of soil warming experiments with a total of 140 measurements from 8 individual study sites.

Site	Location	Latitude	Biome types	Increased T (°C)	Duration	Reference
Harvard Forest (1)	MA, USA	42.50° N	Mixed deciduous	4	1	Peterjohn et al, 1994
Howland Forest	ME, USA	45.17° N	Mixed conifer	5	1	Rustad & Fernandez, 1998
Huntington Wildlife Forest	NY, USA	43.98° N	Mixed deciduous	2.5-7.5	2	McHale et al, 1998
Harvard Forest (2)	MA, USA	42.54° N	Mixed deciduous	5	10	Melillo et al, 2002
TERA	OR, USA	44.33° N	Douglas fir	4	1	Lin et al, 2001
Sweden Boreal	Sweden	64.12° N	Norway spruce	5	2	Eliasson et al, 2005
Oregon Cascade Mountains	OR, USA	43.68° N	Douglas fir	3.5	2	Tingey, et al, 2006
Northern Sweden	Sweden	64.12° N	Norway spruce	5	2	Stromgren & Linder, 2002

C.3.2 Meta-analysis

Meta-analysis was used in this study to synthesize data on soil respiration and soil moisture response to soil warming. The strength of meta-analysis is that it can extract results from each experiment and express relevant variables on a common scale, called the effect size. Means and standard deviation data were selected to calculate the effect size. Hedge's d was chosen as the effect size metric for the analysis. Hedges' d is an estimate of the standardized mean difference unbiased by small sample sizes (Hedges and Olkin, 1985). It is calculated as follows:

$$d = \frac{\bar{X}^E - \bar{X}^C}{S}\left(1 - \frac{3}{4(N^C + N^E - 2) - 1}\right)$$

$$S = \sqrt{\frac{(N^E - 1)(S^E)^2 + (N^C - 1)(S^C)^2}{N^E + N^C - 2}} \qquad (1)$$

where d is the effect size; X^E and X^C the means of experimental and control groups; S the pooled standard deviation; N^E and N^C the sample sizes for the treatments and controls; and lastly, S^E and S^C the deviations of the treatments and controls, respectively. The effect size and confidence interval for each site was computed and weighed to attain the mean effect size. The weighted effect size was calculated as follows:

$$\bar{d} = \frac{\sum_{i=1}^{n} w_i d_i}{\sum_{i=1}^{n} w_i} \qquad (2)$$

where $\bar{d}$ is the weighted effect size, n the number of studies, d_i the effect size of the ith study, and the weight w_i (=1/ v_i) the reciprocal of its sampling variance v_i.

The 95% confidence interval (CI) around these effects was calculated as follows:

$$CI = \bar{d} \pm 1.96 S_{\bar{d}} \quad (3)$$

where ($S_{\bar{d}} = \frac{1}{\sum_{i=1}^{n} w_i}$), $S_{\bar{d}}$ is the variance of $\bar{d}$.

We calculated the averaged d across the years and its variance for each site in the same way as the averaging effects across studies, that is, as the weighted averaged Hedges' d and variance for Hedges' d (see Hedges and Olkin, 1985). Mean differences in the rates of soil respiration between the heated plots and control plots were expressed as a weighted average, calculated as a back-transformed natural logarithm response ratio (see Hedges and Olkin, 2000). Since temperature increases varied throughout the warming experiments, intensity of impacts has been also estimated by categorizing the data of increased temperatures. All meta-analyses were run using MetaWin 2.0, a statistical software package for meta-analysis (Rosenberg et al. 1997).

C.4.RESULTS

C.4.1 Soil respiration

Fig. 1a shows the effects of the warming on soil respiration within the individual study sites. In spite of a large variance due to the differences in environmental conditions and warming methods, soil respiration significantly increased across all sites. The mean effect size ranged from 0.6 for the mixed coniferous forest in east-central Maine to 3.0 for the Douglas fir forest located at the Terrestrial Ecophysiology Research Area in Oregon. Across all sites, the grand (overall) mean effect size was 1.2, indicating a significant response to warming. Thus, soil-warming experiments in the field significantly boosted rates of soil respiration. In general, in the first two years of analysis throughout the study sites, soil respiration was significantly increased by approximately 22.5% by applying experimental soil warming, which is similar to the

results from Rustad et al. (2001). Fig. 2a shows that soil respiration was increased by 29% in the first year and by 16% in the second year. This suggests that under the same experimental conditions, the increase in soil respiration could be lower in the second year than in the first year. The response of soil respiration to soil warming unexpectedly appears to decline with the increase in temperature (Fig. 3), which also occurred in earlier studies (McHale et al., 1998; Rustad et al., 2001).

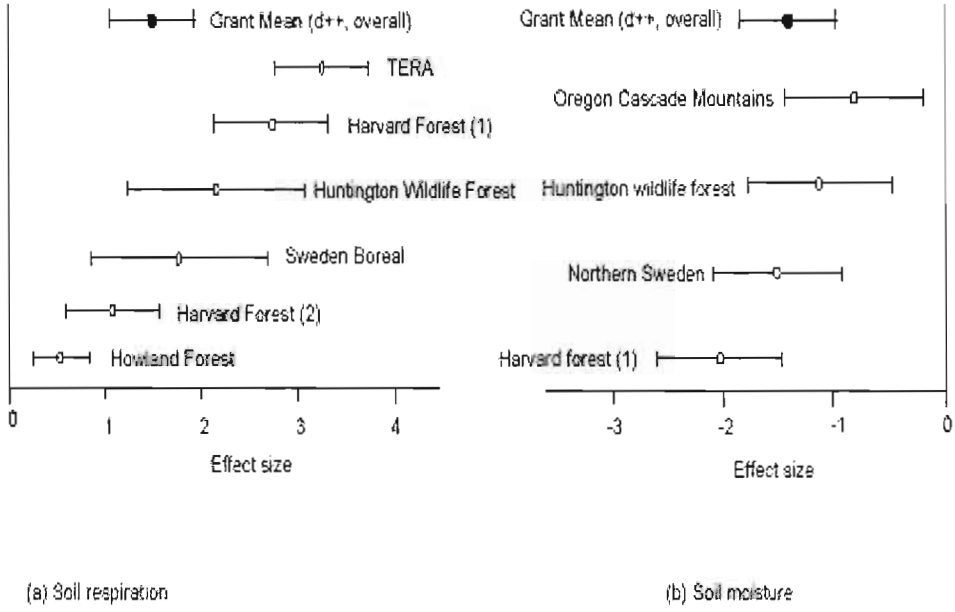

Fig. 1. Responses of soil respiration (a) and soil moisture (b) (mean effect size (d, open circle) and 95% confidence intervals) to experimental soil warming in different study sites. Grand mean effect size (d++, closed circle) for and 95% confidence intervals for each response variable are given at the top of each panel.

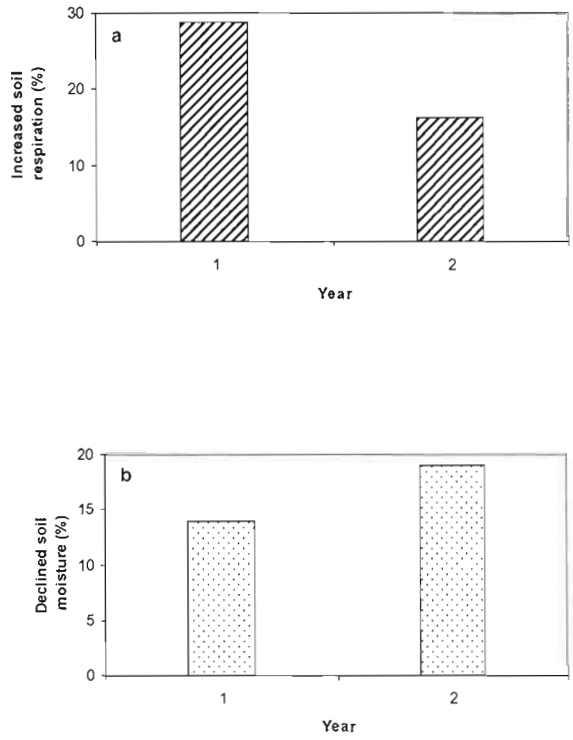

Fig. 2. Increased soil respiration (a) and declined soil moisture (b) after 1 and 2 years of experimental soil warming.

C.4.2 Soil moisture

For soil moisture, the mean effect size varied from -2.1 for the even-aged mixed deciduous forest in the Harvard Forest to -1.0 for the mixed deciduous forest in the Huntington Wildlife Forest. Across all sites, the grand mean effect size was approximately -1.4, indicating a significant and negative response to warming. In general, soil warming significantly decreased soil moisture content across all sites (Fig. 1b). Fig. 2b shows that soil moisture significantly decreased by 14% in the first year and by 19% in the second year under experimental soil warming. Thus, under the same

experimental conditions, the decrease in soil respiration was higher in the second year than in the first year. Across all sites, soil moisture was declined approximately by 16.5% under experimental soil warming, which is consistent with the soil moisture reduction in response to thermal manipulations that has been reported by studies by Peterjohn et al. (1994), Hantschel et al. (1995), and Harte et al. (1995).

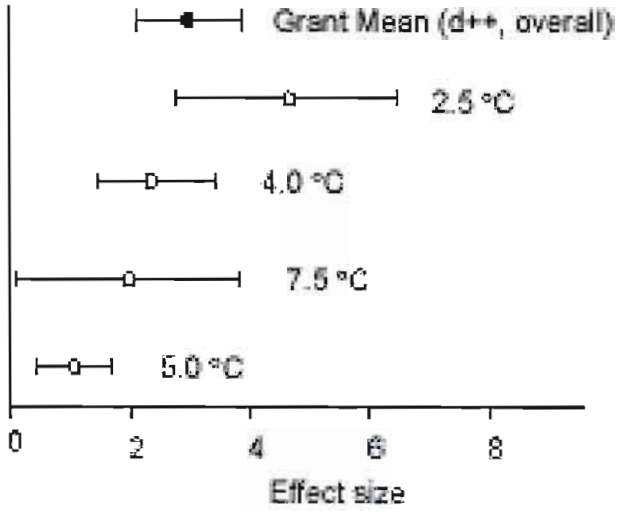

Fig. 3. A response of soil respiration to the range of temperature increase in soil warming experiments (mean effect sizes (d, open circle) and 95% confidence intervals). Grand mean effect size (d++, closed circle) and 95% confidence interval for the response variable is given at the top of the panel.

C.5. DISCUSSION

Previous studies have suggested that a decrease in soil moisture under warming conditions could possibly reduce root and microbial activity, affecting the sensitivity of soil respiration to warming (Stark and Firestone, 1995). In this study, results showed that experimental soil warming decreased moisture content, but did not affect soil respiration in forest ecosystems. Also, several modeling studies have demonstrated that warming stimulates decomposition of organic matter in soils resulting in a decrease in

temperature sensitivity of soil respiration (Gu et al. 2004). Meanwhile, accumulation of more carbon in forest soils may result in a potential loss of large amounts of carbon in the form of CO_2 into the atmosphere.

Several long-term studies demonstrated that the acclimatization trend due to the effects of soil warming on soil CO_2 efflux is attributable to drought (Luo et al. 2001; Melillo et al., 2002), and the fluctuation of other environmental factors, such as substrate depletion (Kirschbaum, 2004). The decline in soil moisture counterbalances the positive effect that elevated temperatures have on litter decomposition and soil respiration (McHale et al. 1998; Emmett et al. 2004). Soil moisture content may become more important over longer time periods. Up to now, short-term studies (1 to 3 years) have far outweighed long-term studies (5 to 10 years) concerning temporal variability in soil respiration. Thus, long-term observations of soil respiration and moisture content are necessary, and to better understand the temporal and spatial dynamics of soil respiration, further studies are necessary so that more soil warming experiments at different spatial scales can be conducted, taking into account more environmental factors and their interactions.Meta-analysis could be used to develop general conclusions, delimit the differences among multiple studies and the gap in previous studies, and provide the new research insights (Rosenthal and DiMatteo, 2001). However, some uncertainties might be brought in this study, since different types of forests joined in the analysis with different structure and turnover patterns of soil organic matter.

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